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EXPERIMENTS IN GRAFTING

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THESE experiments were undertaken primarily to find out whether it is possible by artificial means to induce regeneration in a part that does not regenerate under ordinary circumstances; and secondly to find out what kind of a structure will regenerate from the proximal end of so highly specialized an organ as the limb of a salamander; for, while we know that from the distal end a new limb regenerates we have no information as to what will happen if the proximal end is exposed. Since the latter experiments gave more positive results they will be first considered. As it is necessary to keep the limb alive during the relatively long period required for its regeneration it was necessary to graft it, in a reversed position, on to the same animal.

The following method of grafting was employed. The leg was cut off, the skin loosened around the attached stump and turned back. The stump (composed of muscles, bone, nerves, etc.) was cut off higher up and the skin was then turned back. A pocket was thus formed. Into this pocket the piece cut off was implanted, after being turned around so that its proximal end was directed outwards. The skin was then drawn together by a ligature over the cut end. Since it is desirable to draw the skin completely over the exposed end without, however, pressing too much on the grafted piece, I have found it desir-

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able to cut off a longer piece of the stump than will be required, and then to cut this in half, putting either half back into the pocket, which being incompletely filled, allows the skin to be drawn more readily over the end. The hind-limb being larger was used. The implanted piece, reversed in orientation, consists of bones, muscles, nerves, etc. The skin covering these parts is the old skin with normal orientation. Therefore, at least one element in the complex is not reversed.

In some respects this method of grafting proved unsatisfactory, because the cut end of the stump is so near to the graft that the new material from the stump and that from the graft may easily become mixed, so that the results would be complicated. The shortness of the grafted piece is another source of difficulty, since the short piece may become displaced during the healing of the end. To overcome these difficulties I devised another method, in which however only a single organ has its orientation reversed. The hind leg was cut off at the knee, and the femur removed from the stump for nearly its entire length. It is then shortened by cutting off part of one end, and pushed back into its original position, but with its orientation reversed. Owing to the slightly bent shape of the femur, and its much enlarged knee-end, no chance for a mistake in its orientation is possible. This procedure proved superior to the first, although the problem involved is somewhat different.

At first the large salamander, *Spelerpes ruber,* was used. This is a terrestrial form. Later the somewhat smaller *Diemyctylus viridescens* was used. Both species withstand the operation well and regenerate readily. Serial sections were made of the limbs at different stages of their regeneration.

Regeneration from the Proximal End of a Reversed Piece

An examination of the preparations of those cases in which a cross-section of the limb was implanted in a

reverse direction in the pocket of skin of the same limb shows that as a rule proliferation takes place from the cut ends of the bones, both of the graft and of the stump of the limb. In the majority of cases it is impossible to decide with certainty whether the bones of the new limb originate from one or from both sources. While such a combined formation would be of interest in itself the conditions are such as to make it impossible to assert that both proliferations do actually contribute; for, even if the new material from both sources is continuous with the new material of the regenerating part, we can not be entirely certain that both really take part, however probable this may seem. In a few cases, however, where the skeletal material of the new limb had connected with the proliferating periosteum of the grafted piece there was every indication that the new part was derived from the exposed proximal end. In all cases that have formed a new limb, the periosteum of the cut end of the leg-bones has formed a bar of cartilage connecting their ends with the nearest ends (the original distal ends) of the bones of the grafted piece. Two possible errors make other cases of doubtful value. The short pieces of grafted bones are often turned obliquely, or even sidewise in the end of the limb, due to the contraction of the skin as the end heals, or to changes that take place in the surrounding tissues. In most other cases, the periosteal tissue growing down from the cut end of the leg-bones passes around to one side of the grafted piece, and, with or without receiving contributions from the latter, forms the cartilage of the new limb. In fact, in some cases this can clearly be seen to have taken place, in others, while not so evident, the possibility of such a process exists and renders the result uncertain.

In order to avoid this source of error I adopted the second method of grafting described above. A long piece of the femur was grafted in a reverse position in the thigh. The length of the piece prevented its rotation, and at the same time by increasing the distance

between the distal end of the leg-bone and the proximal (now inverted) end of the graft it was possible to detect with greater precision the source of the material for the new bones. The presence of a single bone instead of two as in the former case also simplified the conditions. Despite these advantages, only a few cases were obtained in which the results seemed to show with great probability that all of the material for the new skeletal parts was derived from the exposed proximal end of the grafted piece. In such cases there was always established a cartilaginous connection between the cut distal end of the femur of the stump and the cut distal end of the grafted piece. The new limb is thus made up of a proximal piece of the femur, connecting cartilage, grafted piece of reversed femur, new tibia, fibula, tarsalia and phalanges from the proximal end of the grafted piece. Evidences of absorption are generally seen in the grafted piece. How far this might ultimately go was not determined.

TAIL IN LEG AND LEG IN TAIL

By means of the skin-pocket-method it is easily possible to graft a short piece of the tail (without skin) into a pocket of the leg, and *vice versa,* a piece of the leg into a skin pocket at the cut end of the tail. I have made a few such experiments with *Spelerpes ruber* not without hopes that from the graft in the leg a tail might develop, and a leg from the end of the tail. The results proved otherwise, for, whenever regeneration occurred, the new material for a new leg came from the cut end of the old leg-bones the proliferating cells passing to one side of the grafted piece and the latter becoming absorbed.

A similar process occurred in the case of a leg grafted in a tail; a new tail and not a leg regenerated. The experiment shows that care must be exercised in interpreting the other cases where the same kind of organ is grafted in a reversed position.

Regeneration after Removing a Bone some Distance from the Cut End

In order to see what would happen if the bones are absent at the cut surface, the hind leg of Diemyctylus was cut off above the knee, the greater part of the femur was removed from the stump, and the skin sewed over the cut end. Regeneration of a new leg was delayed, but took place. The stump of the leg seemed to contract somewhat, so that the cut end of the bone was brought nearer to the cut end of the muscles. The proliferation from the end of the bone must have grown down to the cut surface, and then, extending beyond this, given rise to the material for the skeleton of the new leg. The experiment shows the possibility of the same thing occurring when a grafted piece is pushed aside. Unless the graft block the proliferation from the bones of the stump, these may contribute material to the new limb.

Attempts to Induce Regeneration in the Leg of the Frog

In order to see if regeneration could be induced in adult frogs numerous experiments have been made during three winters. Pieces of the leg were cut off, and grafted in skin-pockets in various ways, but without results. I hoped that the breaking down of such grafted pieces might incite the regeneration process, if its absence in frogs were due simply to some retarding influence in the method of closure of the cut surface as occasionally occurs in pieces of other animals that have well developed powers of regeneration.

Pieces of the leg of tadpoles (without the skin) were also inserted into the leg of the frog without inciting regeneration, but as different species were probably used for graft and stock, successful results were less to be expected. Pieces of the muscles and other tissues of the tadpole's tail were inserted in skin-pockets of the leg of the frog but without effect. Since the tail of the tadpole has remarkable powers of regeneration, it seemed

possible that the presence of such tissue might excite the leg to regenerate, but this did not prove to be the case. Possibly, here also, the difference in species spoiled the result, but this seems unlikely, since it has been shown that young tadpoles of different species may be readily united and form permanent unions.

It is well known that the skin of the frog has excellent powers of regeneration, yet when the leg is cut off it generally ceases further growth after the cut surface has healed over. It occurred to me that the pressure of the skin over the cut end might in itself prevent the further growth of the internal organs. To examine this possibility I cut off the fore-leg turned back the skin, cut off a piece of the stump, and then sewed up the end of the pocket. There was thus left a free space between the cut end of the stump and the end of the skin. Nevertheless regeneration of the limb was not hastened. In other cases agar, or the coagulated white of the hen's egg, was inserted into the pocket, on the supposition that as they were absorbed the regeneration might take place but nothing of the sort occurred. These experiments were undertaken before I became aware of the fact that the fore-leg of an adult frog may actually regenerate, but only after a long time and imperfectly, so that the experiments would be expected at most to facilitate or hasten the regenerative process which however they did not seem to do. In the winter of 1904–05 one frog that lived for several months, floating in the water, regenerated a long outgrowth from the cut end of a fore-leg. The new part had one or two rudimentary finger-like outgrowths, but although the outgrowth was long it was very imperfect as a limb. This frog had had its leg cut off twice, the second time two months after the first operation. In some preparations of Mr. Goldfarb I had seen the great thickening of the periosteum that takes place after several weeks, and this suggested, that if the leg were cut off anew at this time, regeneration might take place. I have also obtained more recently two or

three other cases of regeneration of a limb in this way, and in these the new foot was flat and broad, and plate-like, but with scant evidence of toes. That the regeneration of a new leg is not dependent on this two-fold operation has been shown by Mr. Goldfarb who has also obtained cases of regeneration of the fore-leg of the frog after a single amputation. Since Mr. Goldfarb will describe these cases in detail further description may be omitted here.

The toad, being a more primitive member of the Anura, might be supposed to have greater powers of regeneration, but experiments have been less successful with it than with the frog. The thickening at the end of the bones forms a large knob, as it does also in the frog at first, but in the toad no subsequent changes appear to take place.

Experiments with Lizards

During the summer of 1904, while enjoying the hospitality of the Marine Laboratory of the Leland Stanford University, I carried out many experiments with lizards, but since the results were purely negative they may be given in a few words. In the lizard the tail has the power to regenerate with great facility, but the legs appear to have no power of this sort. I tried grafting parts of the tail in skin-pockets in the legs, in the hope of inciting regeneration. In some cases large pieces were inserted, containing all of the tissues, in other cases pieces of single tissues, muscles, bone, periosteum, etc., were put into the pocket, but without producing the desired result. The lizards were kept alive in some cases for six to eight months without showing any signs of regenerating the leg during this time, but even the tail regeneration is not rapid. It appears, nevertheless, that the regeneration of the leg can not be induced by the presence in it of pieces of other parts of the body that have the power to regenerate.

CONCLUSIONS

Although the experiments undertaken in the hope of inciting regeneration in parts that do not do so ordinarily, or imperfectly and only after a long time, have not given any positive results as yet, still even the negative results are not without a certain theoretical interest. The experiments with the frog showed that the lack of power to regenerate, or only to regenerate imperfectly after a long time, is not due to the pressure of the skin on the cut end of the parts beneath. It is interesting to find that when after several months the internal parts begin to push out a new stump, as sometimes occurs, the skin is then also incited to regeneration, and will form a suitable covering for the parts beneath. It is plausible to suppose that this growth of the skin is due to the pressure of the new part from within. Other factors may also enter into the result, but that the pressure must be the main factor is shown by the failure of the skin to regenerate when other tissues, those of the tail for instance, are present, that have themselves the power to regenerate, but not finding suitable conditions for regeneration fail to form an embryonic knob. In its absence the skin is not incited to regenerate. The fact that the skin does not show any tendency to complete itself alone, although it has the power of regeneration, is important as showing that the possession of this power is not itself a stimulus that will lead to its development. Some other condition is necessary to call it forth, and in this case, that condition seems to be pressure from beneath.

Other tissues in the leg may also have the power to regenerate, but fail to do so unless certain conditions are realized. This state of affairs may lead us to hope that with a better knowledge of the conditions we may ultimately control them, and I trust this may be a first contribution towards that end.

That the muscles in the frog's leg have the power to

regenerate can be shown by cutting from the side of the gastrocnemius a square piece of muscle tissue. In the course of a few months I have found that the muscle regains its size, which seems to be due, in part at least, to the formation of new muscle, although hypertrophy of the remaining fibers may also assist in the enlargement.

There is some indication that the delay in the formation of the new leg in the frog is due to conditions existing in the bones or muscles and, as I have pointed out,[1] it is significant to find that in the vertebrates the loss of power to regenerate a limb appears where cartilage has been changed to bone. The result is not however due directly to the ossification, since the new material is derived from the periosteum and not from differentiated tissue.

Especially interesting is the evidence showing that the introduction of material, itself capable of regeneration (as when the tail-tissue of the lizard is introduced into the leg-pocket) does not incite the leg to regenerate. If the process of regeneration is due to some enzyme, or other substance of this nature, that arises in an injured region, and whose presence incites the new growth, we might hope by introducing pieces of material capable of forming such substances to incite regeneration, but no such result followed. It would be unwise to lay too much weight on negative evidence of this kind, but the results as they stand indicate, perhaps, with some probability, that the primary cause of regeneration is not to be found in this direction.

Finally, to revert once more to the experiments that gave positive results. It has been shown that from the proximal end of a reversed femur new limb bones develop. This result calls for further analysis. It is clear that each level of the limb has the power to regenerate all of the parts lying more distal to it, and in all proba-

[1] The Harvey Lectures for 1906–7.

bility every level has potentially the power also to regenerate all the other parts of the limb proximal to that level. It is difficult to show that a distal part has the potentiality to produce more proximal parts, but the facts make this interpretation highly probable. How much of the distal end regenerates depends in part on its relation to what is left in the stump, and in part on the necessity of forming a distal structure. Between these limits the intermediate parts are laid down. The proximal cut end of a limb must have the same potentiality of forming distal structures as has a distal end and in those cases where the possibility exists of forming either an anterior or a posterior structure, as in pieces of lumbriculus, for example, some other relation must determine that from one end of a piece a head always develops, and from the other end a tail. I have suggested that the direction of the gradations of the old material (as expressed in their differentiation) is the factor that regulates this result. If we apply these same ideas to the special case under consideration we might expect the proximal end of the leg (or any part of it) to regenerate only proximal structures; in other words to complete the proximal end of the femur and produce a scapula at the exposed end of the leg, and, theoretically, one might imagine the further development of a salamander around the scapula as a center. The facts are the reverse. The conditions that determine in the case of the reversed femur what shall regenerate of the various possible ones are not so simple as just described. In the first place, the detachment of the femur from the rest of the limb may soon lead to changes in it that cause it to lose that gradation of materials on which the polarity of the new part depends. There is also the possibility that the polarity of the other tissues may have a counterbalancing influence. But far outweighing these possibilities there is another consideration of greater weight. The special group of tissues found in such an organ as a limb may be capable of forming only one

structure, if they form anything at all, namely, a leg, and not a salamander to take the extreme case. But why always the distal end of the leg and not the proximal, *i. e.*, not femur and scapula? The determination of the distal end rather than the proximal must be due, I think, to the presence of the free rounded knob covered by the new skin which gives the stimulus for a distal structure, and the foot end of the leg is the only possible distal structure that exists for this organ.

The case is parallel to the formation of a heteromorphic tail in the earthworm, that develops, as I have shown, from the anterior end of a piece when cut behind the level of the twentieth segment, or thereabouts. Here also a distal structure develops, but the nature of the material is such that a tail rather than a head regenerates. While polarity, as an expression of the gradation of the materials, is one of the factors that determines a result, it is not the exclusive factor. In Lumbriculus a head forms at the anterior end of a piece at nearly all levels and a tail at the posterior end. Here we must assume that the kinds of materials are so equally balanced throughout the greater length of the worm that the polarity determines the result, while in the earthworm and in the leg of the salamander another condition determines a different result. In the latter cases the kind of material, or the organ-complex, makes it possible for only a tail or a leg to develop at either end of the piece, and the presence of a free end determines that its new structure must be the terminal part, hence a foot in the case of the salamander, and a tail in the case of the earthworm, is regenerated even from a reversed end.

THE PHENOGAMOUS PARASITES

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The object of this essay is to describe in a popular manner the chief characteristics of the known kinds or groups of phenogamous parasites, to show their relation to one another and to normal phenogams, and to discuss their structure and habits with reference to the probable manner of their origination. In order to make a popular statement of the characteristics of each group of these abnormal plants and to discuss them clearly it is first necessary to summarize briefly the elemental structure and physiological characteristics of the normal phenogams. I have chosen to do this in verbal terms a part of which are somewhat unusual, but which are believed to be specially appropriate to discussions of this kind.

The elemental parts of a normal phenogamous plant are root, stem and leaves, the beginning of the differentiation of which structures is distinguishable even in the embryo; and to these are added, at the maturity of the plant, flowers and fruit. Every normal phenogam also consists of two incremental parts, an up-growing and a down-growing part, respectively, the latter entering the soil to form the roots. The normal phenogamous plant performs all its physiological functions within, and for, itself and lives independently of all other plants except in the matter of competition with them for the benefits of soil, moisture and sunlight, but the parasites escape the performance of those functions so far as nutrition is concerned. The normal plants derive the materials for their subsistence and growth from inorganic sources and elaborate them within their own tissues for their own use, producing thereby their new organic substance, but the parasites rob other plants of that substance in its elab-

orated condition. The supply of inorganic material is obtained by normal plants partly in a soluble and partly in a gaseous condition, the former being contained in the food-sap which the roots derive from the soil, and the latter in the atmosphere which surrounds the plant. The function of the root requires a constant accession of moisture, and that function is vital with relation to the other functions of the plant presently to be referred to. The action of sunlight is indispensable in the condensation and elaboration of those inorganic materials into new organic substance. An essential step in that elaboration of new material is the production of chlorophyl, which takes place partly in the bark of the growing branches, but mainly in the parenchyma of the leaves. Fully developed green leaves are therefore among the chief organs of normal phenogams, and their absence from the greater part of phenogamous parasites is due to the inability of those plants to produce chlorophyl. It is for these reasons that chlorophyl is so frequently mentioned in the following paragraphs.

The reproduction of normal phenogams is by two methods, namely, parturital [1] and blastemal.[2] These methods have such relevancy to the subject in hand that it will be frequently necessary to refer to them. The first is the conjugative method and provides for the hereditary transmission of specific and other systematic characters, the geographical distribution of species and the multiplication of individual plants. It is periodically cyclic, the maturation of the seed ending one cycle and the germination of its embryo beginning another. The second is the autogenous method and pertains to the growth and preservation of the individual plant. Its operation is physically continuous during the whole life of the plant, and every bud of the plant is connected with all the other buds by living somatic cells. The horticultural processes of budding and grafting consist of transferring blastemal

[1] Parturio, to bring forth young.

[2] Βλαστος, a bud. These terms are regarded as preferable to "sexual," "asexual," "vegetative," etc., which are often used by writers.

reproduction from one plant to another. They are closely simulated by some parasites in their manner of attachment to the host, but there are radical differences between parasitic attachment and horticultural grafting.

The two incremental divisions of every normal phenogam consists of an epitropic, and an apotropic[3] portion, respectively, separated by the tropaxis. The epitropic portion, beginning with the radicle at germination, enters the ground, divides into roots and rootlets, and establishes the plant in position. This is primary epitropism. The apotropic portion at the same time extends upward, forming the stem and finally the branches, leaves and fruit. This is primary apotropism. The tropaxis is a theoretical disc at, or a transverse section of, the base of the stem from which growth proceeds in opposite directions. Its functional existence as a dividing plane is real and constant during the life of the plant, but it is structurally not clearly definable. That is, no material change of plant-texture occurs at the place where the upward and downward growth diverge, and no obstruction to the flow of food-sap from one to the other portion exists there. Suckers, stolons, sprouts, etc., sometimes spring from roots, root-stalks or tubers, and become new plants. This is secondary apotropism. Roots or rootlets often spring from the stem or branches. This is secondary epitropism. A new or secondary tropaxis is formed in every case of secondary apotropism at the place where the upward growth begins and new roots turn down into the soil.[4]

Such are the leading structural characteristics of normal phenogamous plants, which constitute the mass of

[3] For a full explanation of these and some of the following terms see my article in *Science*, N. S., vol. XII, pp. 143–146.

[4] The terms "hypocotyl" and "epicotyl," meaning below the cotyledons and above the cotyledons, respectively, often have been used by authors to designate the apotropic and epitropic portions, respectively, of the germinating embryo. Those terms are inappropriate for such use because the place of attachment of the cotyledons rarely, and only accidentally, coincides with the place where upward and downward growth diverge, and the two places are often far apart. A case in which they are far apart is illustrated by the plantlet of Convolvulus as shown by Fig. 6, on page 28.

the green vegetation of the earth. Abnormal phenogams constitute only a very small proportion of the great mass of vegetation, and yet the aggregate number and variety of their forms is really very great. Three general kinds of abnormal phenogams are recognized, namely, parasites, saprophytes and symbionts. They have certain characteristics in common and often are visually similar, but they differ materially from one another in the manner of procuring their subsistence, and the habit of each of them in that respect may be either partial or complete. That is, a phenogam may be partially parasitic, saprophytic, or symbiotic, and partially normal; or parasitism may be associated in one and the same plant with saprophytism. While my chief object is to discuss the parasites, it will aid in defining their characteristics to present a brief statement of those of the two other kinds of abnormal phenogams.

Saprophytes derive their subsistence from dead organic matter in the soil which has not reached the stage of full decomposition. That matter yields a soluble portion to the food-sap which the plant obtains by its roots in the usual manner and, after some reelaboration, that portion is applied by the plant as new organic substance in the building of its tissues. Saprophytes, like vultures, hyenas and epicures, take their food in a partially decomposed condition and thrive upon it. Doubtless many plants that are properly regarded as normal are really in part saprophytic when their roots have access to organic manures, but only completely saprophytic phenogams are here referred to. It is claimed by some investigators that completely saprophytic phenogams sometimes produce chlorophyl and develop green leaves, but those here discussed produce no chlorophyl, develop no functional leaves, and are therefore not green in color. Their reproduction, both parturital and blastemal, is normal and they grow from their roots in the soil like normal plants, with none of which are their vital relations antagonistic. Completely saprophytic phenogams, which only are now particularly referred to, are comparatively rare, especially in ordi-

nary soils. They are mostly confined to swampy and other moist soils that contain much decomposing vegetable matter, and to shady positions. It may be suggested that the abundance of disintegrating organic material contained in the soil in which these completely saprophytic plants grow furnishes so large a supply of material which is still useful for assimilation in the production of new organic substance that the entire leaf-function, including the production of chlorophyl, is suspended as being superfluous, and that this habit has become permanent and hereditary.

Completely symbiotic phenogams live in enforced vital union with a fungus which adheres to and covers its roots, and through which it derives all its soil-subsistence. The roots being entirely enveloped, their normal function is destroyed and the fungus also assumes the office of purveyor of nutriment. As do other fungi, it obtains that food-material from decomposing organic matter in the soil and transfers a portion of it to its consort through their surfaces of contact. Although that food-material, when obtained by the fungus, is partially decomposed, and is received at second hand by the captive phenogam, the latter thrives upon it, and, its above-ground portion being free, the functions of vegetative growth and reproduction are normally performed. Its leaves, however, are abortive or functionless and never green in color, for completely symbiotic phenogams do not, and do not need to, produce chlorophyl. Their failure to do so is doubtless a direct result of the condition which is imposed upon its roots by its fungus consort. The vital relations of these strangely modified phenogams with other plants are normal, but their condition with relation to the fungus is apparently that of pitiable captivity. The usurpative control of their nutrition by the fungus suggests that these phenogams did not originate as symbionts by a predilective departure from a self-supporting condition. Partial symbiosis of fungi with phenogams is not uncommon and is understood to be, at least in many cases, mutually beneficial, but it has only incidental relevancy in

this connection. One can hardly doubt that the complete symbiotic condition of those plants has been imposed by the aggressive increase of the fungus from its original condition of partial symbiosis, but the phenogam so fully acquiesces in it that the deficiencies of structure and function which its imposed condition entails have become harmonious with that condition and hereditary. Even the embryo, at least in the case of Monotropa, or Indian pipe, and probably also in that of Sarcodes, or the snow plant of California, has lost its differentiation into cotyledons and plumule. This is a significant coincidence with a similar condition which prevails in the embryo of many parasites, as will be shown in following paragraphs.

Examples of complete symbiosis are few among phenogams, the most common case being that of Monotropa. All the older botanists believed, and some of them so stated in their text-books, that the species of that genus are parasitic upon the roots of woody plants. Later authors often have stated that Monotropa is saprophytic, but still later investigators have demonstrated that the plants of this genus are completely symbiotic. It will be a disappointment to the older plant-lovers not to find their familiar acquaintance, the Indian pipe, discussed among the parasites on the following pages, but the facts which have been stated require its omission there.

Whatever view one may take concerning the two kinds of abnormal phenogams that are briefly defined in the preceding paragraphs, he instinctively regards the parasites as a criminal class in the great community of honest plants. Their methods of parasitism are so varied, and each method is prosecuted with such vigor and constancy, that it is necessary to review them with reference to those habits rather than to similarities and differences of systematic structure. They all are at least acquisitive in their relations with other plants, and some of them are vigorously aggressive and raptorial. They all derive new organic substance from other plants, always from living ones, and apply it directly in the building of their own tissues. Some of them are annual, and some

perennial. Some are herbaceous, and some woody. Some of them attack only the epitropic, and some only the apotropic, portion of their host. Some are only partially parasitic, obtaining only a part of their subsistence in that manner, but a large number are completely parasitic, and thus obtain their entire support from other plants. The former obtain a part of their subsistence from the soil as normal plants obtain all of theirs. They also develop leaves and produce chlorophyl, but the complete parasites, with exceptions to be mentioned, develop no functional leaves and produce no chlorophyl, for completely parasitic plants do not need to produce it. New organic substance, elaborated as already has been mentioned, is of course necessary to the existence of the normal plants which produce it. It is no less necessary to the existence of the parasites, but they, not being able, or not predisposed, to produce it for themselves, obtain it by robbery from other plants. All of them are so depraved that they acquire special hereditary habits of rapine, modify their structure, and even develop special organs with which to accomplish their thefts. The deficiencies and modifications of structure are correlated with the respective kinds of parasitism, and they are invariable and heritable. Even the embryo of some of them is structureless, not being differentiated into cotyledons, radicle and plumule. Indeed, some of the most vigorous of the parasites originate from embryos that apparently represent only a moiety of the normal phenogamic embryo.

The leaves of normal phenogams are properly regarded as the chief organs concerned in the production of chlorophyl, but if my assumption is correct that the agency of a structural root is a precedent necessity in normal cases of such production, the functional leaflessness of a parasitic phenogam is a direct consequence of its rootlessness. That is, because a rootless phenogam can produce no sufficient quantity of chlorophyl, and because it procures its new organic substance by theft, it has no use for leaves. Therefore, those leaves which it morphologically inherits remain undeveloped or functionless. This is the

condition of complete parasitic phenogams, but those which are only partially normal supplement their honest gains by theft. They are all robbers, and obtain new organic substances from their hosts by methods which resemble grafting, budding and leeching, respectively. In the first two cases mentioned the embryo of the parasite is thrust into the living tissue of the host from which the resulting parasitic plant draws its nourishment, much as do the bud and scion in cases of budding and grafting. In the other case special organs, namely, haustoria, are developed as instruments of robbery. These organs serve to draw new organic substance in liquid form from normal plants, and they are as indispensable to the parasite which possesses them as are roots to normal plants. They are produced as small outgrowths from different parts of different parasitic species, sometimes upon the roots and sometimes upon the stem and branches. They are of wart-like, discoid, globular, or more or less irregular form, and are sometimes single and symmetrical, but oftener in groups or clusters and shapeless masses. When single they are sometimes sessile and sometimes terminal on slender pedicels. They attach themselves by their free surface to the host, and so burrow into its subcortical and subcortical tissues that the growing cells of both plants are intimately commingled. Acting like suckers, they withdraw in liquid form the new organic substance which the host had prepared for its own use, much as a leech extracts blood from its victim. The haustoria of parasites are comparable with roots of normal plants because, like roots, they are the instruments by means of which the plants obtain necessary supplies, but true haustoria are not roots nor morphological representatives of them.

The foregoing remarks apply mainly to the general characteristics of the parasites as compared with saprophytes, symbionts and normal plants. The special characteristics of the parasites are grouped and briefly summarized in the following synopsis. In remarks which follow each synoptical statement some of the more con-

spicuous of those extraordinary habits which members of the various groups possess and which have become constant and hereditary will be shown. Many of those habits are of wonderful character, and one almost feels that he is dealing with sentient beings of great cunning and lawlessness rather than with vegetal forms.

The phenogamous parasites are so aberrant as regards both their structural and vital relations to other plants and to one another that it is difficult to classify them. Indeed, there is no logically recognizable correlation of any of the parasitic characters of the species in question with those which pertain to systematic classification. The following synopsis, prepared for the present occasion only, embraces seven groups the characterization of which is, so far as practicable, based upon the manner of parasitism of the members of the respective groups and upon the peculiarities of their life history, especially that phase of it which pertains to germination.

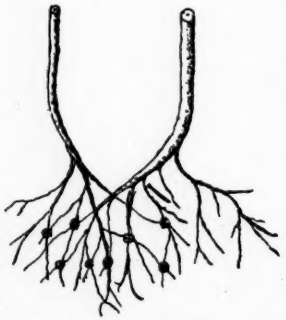

FIG. 1. Diagrammatic pen-sketch, showing the position of haustoria at the places of contact of roots of the parasite and its host. The haustoria are represented by small circles, which are, however, proportionally much larger than natural size.

GROUP I

Seeds germinate upon the ground. Embryo differentiated into cotyledons, radicle and plumule, like normal embryos. Like normal plants also those of this group produce chlorophyl. A part of their roots are attached by sessile haustoria to roots of other plants, from which they obtain ready-made organic substance in liquid form, and a part of them obtain food-sap from the soil in the normal manner. Therefore their parasitism is only partial. Examples: Euphrasia, Pedicularis, Castilleja and many others.

The parasitism of the members of group I, which are

mostly perennial herbs, is confined to limited underground pilfering. It is the simplest form of phenogamous parasitism but it is as persistent and hereditary as are the more complex forms, and it is practised by a large number of genera and species which have numerous near normal relatives. Because they have normal roots and leaves and produce chlorophyl they begin life with the ability to procure an honest living, but they seem to be unable to resist their inherited parasitic inclinations. The development of haustoria at the points of contact of their roots with roots of other plants begins after their germinative birth from a normal embryo and an early stage of full self-support obtained from the soil; but so firmly fixed is the habit of pilfering in these plants that when they have been experimentally forced to live honestly in good soil, but beyond the reach of roots of other plants, they have ceased to thrive, as if they were insufficiently nourished.

Group II

Parasites attached to the stems and branches of woody hosts upon the bark of which the seeds germinate, being affixed there by their glutinous covering. Embryo differ-

Fig. 2. Pen-sketch of a branch of *Viscum album*, the Old World mistletoe; much reduced in size. *A*. Diagram showing the mode of attachment of the parasite to the host by the sinkers.

entiated into cotyledons, radicle and plumule, and the plant consists of both epitropic and apotropic portions. The latter is differentiated into stem, branches, leaves and fruit, as in normal plants. The leaves, and also the bark of the stem and branches, contain chlorophyl which is produced by the plant itself. The parasite is attached

to the host by "sinkers" which consist of specially modified, but true, rootlets, although in function they simulate the haustoria of other parasites. The sinkers penetrate the bark of the host and obtain nourishment for the parasite from the growing tissues beneath it, much as food-sap is obtained from the soil by normal plants. The parasitism is complete. Examples: The mistletoes.

The members of group II are perhaps the most generally known, at least by name, of all the phenogamous parasites. The family to which they belong, the Loranthaceæ, is a large one, and some of its members differ considerably from the typical forms of mistletoe. Only *Viscum album* of the Old World, and *Phoradendron flavescens*, of the New, however, are chosen to represent group II on this occasion. These mistoes differ from the members of all the other parasitic groups in being perennial woody parasites upon woody hosts, and also in their method of parasitism. That method is peculiar because it simulates grafting, because morphologically its "sinkers" are true rootlets and not haustoria, and because the passage of sap from host to parasite is by those rootlets and not through such harmoniously joined cells as are formed between the graft and its stock. Mistletoes have been known to become parasitic upon other mistletoes, but in their choice of a host they usually give preference to trees that are not botanically related to them. Their structure, both embryonal and mature, is so nearly normal that one might believe them capable of

FIG. 3. Pen-sketch of a branch of *Phoradendron flavescens*, the New World mistletoe; two fifths natural size.

leading an honest life in the soil, but so firmly is their predatory habit established by heredity that they never do so. Their seeds will germinate successfully only on the bark of living trees, and their embryos, although structurally perfect, are evidently unable to develop in the soil. When germination of the seed begins the radicle pierces through the dry bark of the host as if driven by some extraneous force; and it sometimes enters the bark of a branch from its under side, showing that gravity is not that impelling force. It lifts the strong bark by its increment beneath, and sends the sinkers into the growing layers. The cells of those layers and the cells of the sinkers become vitally commingled much as do the somatic cells of the scion and stock in common grafting, but not quite so harmoniously. This parasitic root-grafting is remarkable because the parasites and their usual hosts differ from each other in botanical relationship far more than do any scions and stocks that can be artificially grafted with success.

Because the mistletoes obtain full nourishment from their hosts their parasitism is complete, and yet, unlike other completely parasitic phenogams, they produce chlorophyl in their own tissues. The production of chlorophyl by the mistletoes is apparently due to the fact that they have retained morphological representation of true roots, notwithstanding their parasitism. While the mistletoes have retained more of the structure and functions of normal plants than have other completely parasitic phenogams, their draft upon the vitality of their hosts is great, and it doubtless would be more apparent if the latter were less vigorous.

Group III

Seeds, having the embryo differentiated into cotyledons, radicle and plumule, germinate upon the ground and there produce plants which begin to grow in the soil in the normal manner. By their earlier roots they are partially parasitic after the manner of group I, but, suddenly, the whole plant becomes epitropic and enters the soil bodily by burrowing, much as does the peanut pod

when ripening. It there branches freely, assuming the form of a large complex blanched rootstock, and becomes wholly parasitic. It passes its whole mature life under ground except that some of its branches rise above ground to flower, but those branches always die when the fruit has ripened. Its earlier parasitism is by sessile haustoria, which are soon discarded, and its later parasitism is by haustoria-tipped tendrils, sometimes erroneously

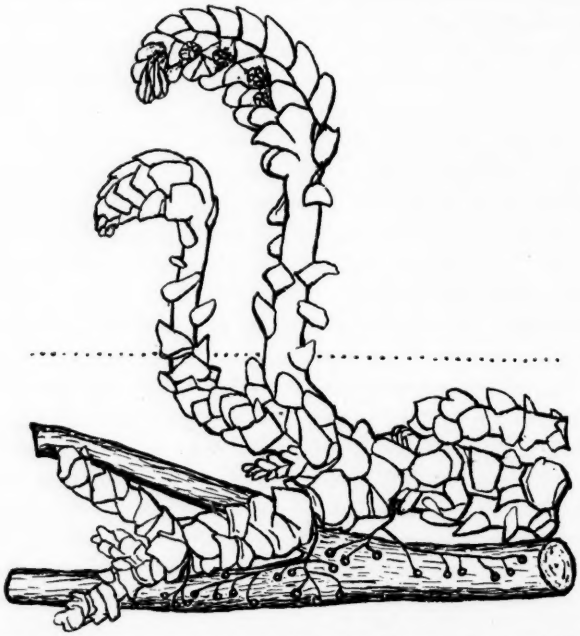

FIG. 4. *Lathræa squamaria;* pen-sketch after Kerner. The dotted line represents the surface of the soil. Only a small part of the underground stems and branches is shown in the figure, together with tendrils bearing the pediculate haustoria.

called roots or rootlets, which issue from the underground stem and branches. No chlorophyl is produced and no functional foliage or functional roots are developed after the plant begins its burrowing. Example: *Lathræa squamaria.* This group has no known American representatives.

The species which has been chosen to represent group III is a European form and is quite distinct in certain respects from even its nearest botanical kindred, and it possesses habits that for variety and extent of abnormality are not surpassed, and apparently not equalled, by any other plant. It begins life normally, as do members of group I, which it then closely resembles. The presence of chlorophyl in the plumule of its plantlet and the development of early rootlets seem to indicate an honest destiny for the plant, but its subsequent acts almost suggest its utter abandonment to a groveling life.

Group IV

Seeds germinate upon the ground, producing an annual herbaceous plant. Embryo filiform and coiled within a mass of albumen in the seed; not differentiated into cotyledons, radicle or plumule. The resulting plantlet retains the filiform structure of the embryo without differentiation, except that the part which becomes the lower end of the plantlet is slightly enlarged. As the embryo uncoils the larger end enters the ground a little, but sends no rootlets into the soil and therefore derives no true food-sap therefrom. The smaller end points upward and the plantlet elongates as a single thread-like stem until it comes in contact with some freshly growing part of another plant. It there attaches itself by quickly developed haustoria, derives from the helpless host its first sufficient nourishment, and becomes a branching vine. It then reaches out for other hosts by more or less numerous branches, and the part below the first haustorial attachment quickly withers and dies. The branches grow rapidly and bear an abundance of flowers and seed. The plant never naturally produces chlorophyl, and develops neither true roots or functional foliage. The parasitism is complete. Examples: Cuscuta of many American and European species, and Cassytha of many Australian, New Zealand and East Indian species.

The members of groups I, II and III are all developed from perfect embryos, like those of normal plants, their

parasitism and abnormal structures being developed after germination. The remaining four groups are not only deficient in structure at maturity, but they originate from embryos which are also deficient in structure. The first of those four groups to be considered is especially represented in our country by the genus Cuscuta which contains many species, commonly known as dodder. They are often found growing plentifully in fields, thickets and waste places during the summer months, their yellowish tangled masses making them conspicuous among the green vegetation. The embryo of Cuscuta gets very little sustenance from the albumen which envelops it in the seed because the seeds are small; and it is because the plants develop no roots that they get no real nourishment from the soil. Nevertheless, the plantlet grows rapidly, somtimes to several inches in length, before it reaches a host; and although it is so slender it possesses great vegetative vigor. This vigor is conspicuously observable in the subsequent growth of those species which often profusely festoon shrubbery, and even trees, securing their hold upon, and their sustenance from, the tender twigs by means of their haustoria. Other species no less vigorously attack the smaller plants and field crops with which they come in contact.

FIG. 5. *Cuscuta Europæa;* parasitic on a hop vine. Sessile haustoria are shown at places of contact of parasite and host.

The parasitism of Cuscuta differs from that of the other groups in being effected by climbing as a vine from plant to plant, and by lateral haustorial contact of the stem and branches of the parasite with those of the host. In the case of the other groups whose parasitism is aboveground the success of the depredating plant depends upon the propitious position which the seeds may accidentally

obtain; but the plantlet of Cuscuta, after its germination upon the ground seems, by the movements of its free end, to start out in search of opportunities. It adjusts its mode of life to prevailing conditions by delaying its own germination about a month later than that of its prospective victims of annual growth, and it is not discouraged by failure of its first effort to find a host. In that case it falls down upon the ground, shriveled and apparently dying, but if soon, or even within a few weeks, some belated normal plantlet should spring up near it, or some growing branch should droop and touch it, the victim is quickly seized upon by the apparently dying plantlet. Such tenacity of life and apparently dominant purpose in a slender, organless mass of vegetable cells is no less than marvelous.

Because the plantlet of Cuscuta develops no root or rootlets it evidently possesses no real representation of the epitropic portion of a normal plantlet, or at best, not more than a moiety of it which lies immediately subjacent to the tropaxis. The rapid upward growth of the filiform plantlet indicates that at least a considerable part of the apotropic portion is therein represented. Moreover, because it has no cotyledons or plumule it follows that the entire plantlet of Cuscuta represents only the stem of the normal plantlet, or that portion of it which comes between the cotyledons and the uppermost rootlets. The accompanying diagram, Fig. 6, illustrates the foregoing statement.

The upper end of *B*, Fig. 6, not reaching above the upper dotted line, indicates that the plantlet of Cuscuta possesses no representative of either cotyledons or plumule. Its downward extension a little below the lower dotted line similarly indicates the fact that its lower end enters the soil a little way, but that it does not represent enough of the epitropic portion of the normal plant to give origin to a root, or any rootlets. This comparison shows that the whole plantlet of Cuscuta represents only the stem of the plantlet of Convolvulus.

The descriptions which have been given in the preced-

ing paragraphs of the structure, germination, life habits and method of parasitism of Cuscuta apply in every important detail to Cassytha. Even the general aspect of the latter plants is such that an American or European seeing them for the first time instinctively regards them as dodders. Nevertheless the structure of their florescence and fruitage leaves no room for doubt of their close

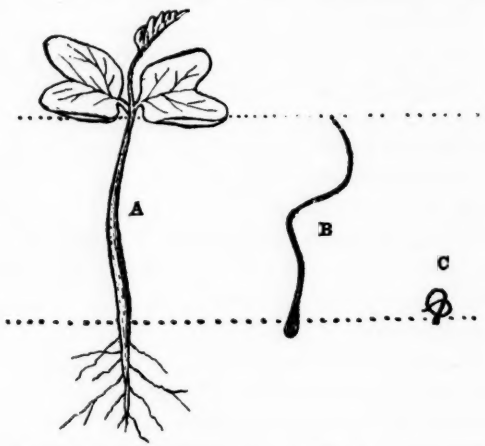

FIG. 6. Diagraphic illustration of the relation of the embryo and plantlet of Cuscuta to the plantlet of Convolvulus.

A. An early plantlet of Convolvulus, with its first root and rootlets, its stem, cotyledons and the first leaf of the plumule, not yet expanded.

B. The filiform plantlet of Cuscuta of nearly the same stage of growth from the seed as *A*.

The upper dotted line crosses *A* just a little below the place of attachment of the cotyledons. The lower dotted line represents the surface of the soil and also the position of the tropaxis of *A*.

C. Embryo of Cuscuta, at the beginning of germination. Much enlarged.

relationship to the Laurel family, while all the species of Cuscuta are nearly related to the Convolvulaceæ.

GROUP V

Seeds germinate upon the ground. Embryo filiform and not differentiated into either cotyledons, radicle or plumule. Its protruding end, or offshoot, penetrates the soil after the manner of a radicle, sometimes to the depth of several inches, but as it sends off no rootlets it derives no true food-sap from the soil. The upper end, or that

which in the normal embryo would bear the plumule, is not developed. If the descending end comes in contact with no living root of another plant the whole embryo dies, although the soil may be abundantly fertile. If it reaches such a root it becomes attached to it and develops a tuberous mass at the place of contact. From this mass spring outgrowths which penetrate the bark of the root-host and blend intimately with the growing layer beneath it, where they act as haustoria. In this mass, also, by a kind of blastemal germination, buds, or substituent plantlets, are formed which produce the flowering stems. No functional foliage and no true roots are developed, and no chlorophyl is produced.

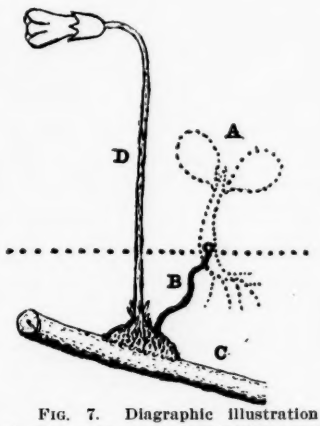

FIG. 7. Diagraphic illustration of the manner of germination and florescence of the broom-rape family, and of the structural relation of its embryo to the normal dicotyledonous embryo.

A. Dotted outline of a normal plantlet introduced only for comparison.

B. Offshoot of a broom-rape embryo. The upper moiety only may be regarded as representing any part of a normal plantlet, and that represents a portion of the stem. The lower portion of the offshoot is spirally prolonged underground, its free end becoming attached to the root-host by a tuberous enlargement.

C. The root-host.

D. Flowering stalk of *Aphyllon uniflorum* springing from the tuberous end of the offshoot. The horizontal dotted line indicates the surface of the soil.

The parasitism is complete. Examples: the broom-rapes and related genera.

The parasites of group V belong to the Orobancheæ, the broom-rapes being chosen as typical members. They are vigorous in their growth and aggressive in their parasitism, some of them being very destructive of cultivated crops; especially hemp and tobacco. Like Cuscuta they delay their own germination until their prospective victims have germinated and grown sufficiently to serve their purpose. The seeds of those species which are parasitic

upon cultivated crops seem sometimes to remain in the soil without germination more than one season, and to germinate when a new cultivated crop is planted. The accompanying figure represents the manner of germination of a member of group V and the growth of its flower stem.

Figs. 5 and 7 respectively represent two parasitic plants which, although they originate from physically similar embryos, are so widely different in their mature structure and habits that the following comparison is thought to be desirable. The seeds of both these parasites germinate upon the ground, but the resulting plantlet of one of them grows upward and that of the other downward, in search of a host. The plantlet of Cuscuta grows upward, which is attributed to the assumed fact that its embryo possesses a considerable representation of the apotropic portion of a normal plantlet, and little or no representation of the epitropic portion. No part of the broom-rape embryo grows upward, presumably because it possesses no representation of the apotropic portion of a normal embryo. Its whole embryo seems to represent only a moiety of the stem of a normal plantlet which lies subjacent to its tropaxis and above its rootlets. The bud from which springs the flowering stalk of broom-rape is not a part of the embryo proper, as is the plumule of the normal embryo, but a result of secondary germination.

GROUP VI

Seeds germinate only above ground and, like those of the mistletoes, only upon a living woody host; usually upon the stem and branches, but sometimes upon exposed roots. Embryo filiform and without either cotyledons, radicle or plumule. No true roots or functional foliage is developed, and no chlorophyl is produced. The embryo, by its distal or protruding end, when emerging from the seed, sharply and vigorously penetrates the bark of the host and sends haustorial processes into the cambium layer, and even into the alburnum. A single flower, some-

times sessile and sometimes having a short stem, issues from the host at the place of entrance of the embryo. The parasitism is complete.

Examples: The rafflesias and related forms.

One of the most remarkable characteristics of group VI is that the individual plants of many of its species reach the lowest structural limit of the phenogam. That is, each one of such plants consists of a single flower which is sessile upon the bark of the host, or apparently sometimes upon its cambium layer. In other cases the plant consists of a short, single scaly stem besides the flower. The sessile species are examples of flowering plants reduced to the flower alone, assuming that the haustorial processes at its base represent the torus, as they seem to do. While the normal phenogam consists of root, stem and leaves, all of which are necessary to serve the purpose of the coming flower and fruit, the sessile Rafflesias throw the responsibility of all else upon the host and furnish only the reproductive organs for their own perpetuation. They serve that purpose effectively, however, although they are rootless, stemless, branchless and leafless plants. And yet they are no more lacking in vitality than are the most vigorous members of the vegetable kingdom.

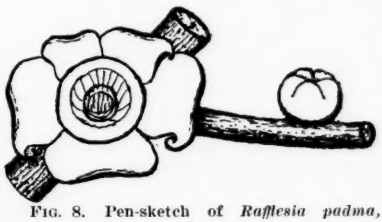

FIG. 8. Pen-sketch of *Rafflesia padma*, together with an undeveloped bud; sessile upon a branch of its tree-host. This species attains a diameter of eighteen inches when fully expanded in flower; but that is only half the diameter of the largest species of *Rafflesia*.

Although the seeds of Rafflesia, like those of the mistletoes, germinate upon the bark of a woody host, their embryo is not of normal structure, as is that of the mistletoes, but is simple and filiform, as is that of groups IV, V, and VII. Because the embryo of Rafflesia is not differentiated, and therefore has not a true radicle; and because it is not able to germinate upon the ground, it is assumed that the protruding end of its offshoot does not represent

the radicle of a normal embryo. If this assumption is correct it follows that the plant is destitute of normal epitropism and that the force with which the offshoot of the embryo pierces the bark and growing wood of the host is an abnormal and violent form of epitropism. It is also assumed that because the embryo of Rafflesia has no plumule the flower does not represent primary apotropism for the plant, but abnormal secondary apotropism as does that of the broom-rapes. The remarkable plants which constitute group VI are divided into many well-defined species and a considerable number of genera. Some of them bear the largest flowers that are known among plants, the largest being more than three feet in diameter, but some are very small. All are natives of warm climates, mostly of Asia, Africa and the adjacent islands. A few American species are known, all of them small. One very small species which is found in Texas and Mexico is sessile in great numbers upon a papilionaceous shrub, and is hardly more than one eighth of an inch in diameter when in full bloom.

GROUP VII

Group VII consists of a remarkable and varied series of tropical and subtropical phenogamous parasites known as the Balanophoreæ. Some of them have large and showy flowers, and some of them have so great resemblance to fungi that the older botanists regarded them as such. All of them are parasitic upon roots of woody hosts, beneath soil which is usually rich in vegetable mold. The seeds germinate upon the ground. The embryo is not differentiated into cotyledons, radicle and plumule, but it is filiform as is that of groups IV, V and VI, and its offshoot penetrates the ground in a manner similar to that of the broom-rapes. In the manner of their germination and in the underground origin of their flowering stems from a tuberous or amorphous mass, these plants also resemble the broom rapes; but in their florescence and fruitage they are very different. They produce no chlorophyl and they are all without either true roots or functional leaves,

although some of them have moderately large, scaly representatives of leaves.

There are probably other forms of phenogamous parasitism, but the seven fore-mentioned groups are the best

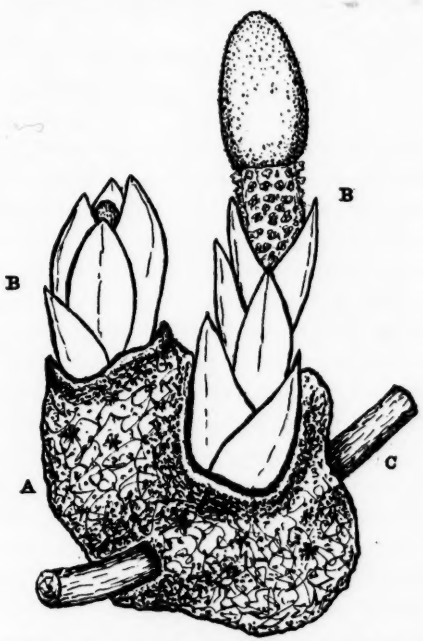

FIG. 9. Pen-sketch of *Balanophora hildenbrandtii*, a native of the Comoro Islands, off the east coast of Africa. After Kerner. One quarter natural size. The leaves of this species, although large, are scaly and not functional.

A. Amorphous, fleshy mass. *B, B*. Flower stems springing from the mass. *C*. The root-host.

known, and they serve to show that they are all depraved members of the class phenogams, and not predatory members of a separate class.

PRELIMINARY REPORT ON AN INVESTIGATION OF THE SEASONAL CHANGES OF COLOR IN BIRDS

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IT is a well-known fact that the males of many species of birds assume a special nuptial plumage at the beginning of the breeding season, sometimes radically different from the plumage of the winter. Especially marked examples are scarlet tanagers (*Piranga erythromelas*), bobolinks (*Dolichonyx oryzivorus*), and certain weaver birds of the genera Vidua and Pyromelana.

We know that the native birds mentioned above lose their brilliant breeding plumage in the early fall and assume a winter dress approximating that of the female. When we consider such a case as the scarlet tanager and the summer tanager (*Piranga rubra rubra*), the former changing annually from scarlet to green, the latter remaining scarlet at all seasons, we have an interesting difference in two closely related species giving definite data from which to work. The problem which I have set myself, and at the solution of which I have made but the merest beginning, is, What is the cause of, or what factors determine, this seasonal change in the males of the scarlet tanager and the bobolink?

So unbroken is the field of research in all such problems as this that the most hopeful way of working is to clear the ground by gradually eliminating all negative factors, and thus narrowing down to the important dynamic qualities of the environment.

On hastily reviewing the field, the following factors have occurred to me as being the most important in bringing about, either directly ontogenetically, or indirectly phylogenetically, seasonal change of color:

General condition of the bird's body—whether fat or thin.

Food—whether vegetable or animal.

Blood pressure—whether raised or lowered.

Sexual organs—whether active or inactive.

Inheritance.

Temperature—heat or cold.

Conditions of humidity or aridity.

This list is of course merely tentative, and the factors enumerated are by no means equal, and some are dependent on others. But they represent what I selected when first I began the experiment detailed below, as a convenient review of the field before me.

This experiment concerns only factor number one, the condition of fatness or thinness of the bird's body and its influence on moult and indirectly on the sequence of annual changes of color.

We know that birds, such as bobolinks and tanagers, after the cares of the breeding season are always thin and in poor condition. The externally worn and bedraggled condition of the feathers is reflected in the physically deeper part of the body, and the keel of the breast-bone—that true index of a bird's condition—often is very conspicuous under the skin of the breast. Not until the fall moult is past do the birds improve much in condition and then they become unusually fat. I think that these few facts hold true of most birds.

Fat is something to guard against in captive birds, and in the Zoological Park I find it necessary to have a weekly examination made of many of the small birds; this being a matter of regular routine. Birds from the various cages are caught and carefully examined, and the proportions of the food ingredients—fat-producing and the opposite—are regulated according to the condition of the birds.

One year ago last summer I took full-plumaged specimens of male scarlet tanagers and bobolinks in full song and plumage and put them under careful observation.

None of these birds had been allowed to breed, and so, although it was rather late in the year, they were still in the height of vocal and physical condition. They were all tame, and although during the period of experimentation they were confined in rather small cages, each bird in a space 12 x 12 x 24 inches, yet their plumage remained in almost perfect condition.

I began gradually to cut off the supply of light and slightly to increase the amount of food. This caused a corresponding decrease in activity of the birds, and an almost immediate increase of weight. The danger of obesity in caged birds is that any excitement or sudden fright may cause a blood vessel to break, or in some other way bring about death from apoplexy. Consequently I kept the tanagers in a room where they were never disturbed and where no noise ever made possible the chance of an untimely end.

A month later when the time for the fall moult arrived, the birds were living "the simple life" in a dim illumination and, although consuming a normal amount of food, were exercising but little. The time for the fall moult came and passed and not a single feather was shed. The cages were made of mosquito-netting wire and would have confined any moulted feathers. In addition to this, the birds were examined every third day, and nowhere on the body was there any sign of moulted or of new, incoming feathers. On blowing away the plumage from the breast, the yellow sub-cutaneous layer of fat could be distinctly seen.

In brief, the birds skipped the fall moult entirely and appeared to suffer no inconvenience whatever as a result. As far as appearance went they were in perfect health, showing only the symptoms of inactivity produced by an excess of adipose tissue. Early in the experiment the songs of the birds diminished and finally died away altogether, and when a good layer of fat had been acquired the birds seldom uttered even a chirp.

From time to time a bird was gradually brought into

the light for a week or two and meal-worms were added to its diet. This invariably resulted in a full resumption of song. Even in the middle of winter a tanager or a bobolink would make the room ring with its spring notes and with this phenomenon was correlated a slight decrease in weight. This phase of the experiment could not be repeated indefinitely, however, for the song period seemed limited, just as it is under normal conditions, although the nuptial plumage remained unchanged throughout the winter. As one of my keepers pithily put it, "We have their calendar twisted backward."

I found that a sudden alteration in temperature—either lower or higher—wrought a radical change in the physical metabolism of the birds. They would stop feeding almost altogether, and one tanager lost weight rapidly. A few feathers on the neck fell out, and in the course of some two weeks this bird moulted almost every feather and came strongly into his normal winter plumage of olive green. The metabolism set up by the change in temperature, in its extent and rapidity, seems comparable only to the growth of a deer's antlers.

Early in the following spring individual tanagers and bobolinks were gradually brought under normal conditions and activities, with quick result: just as the wild birds in their winter haunts in South America were at that time shedding their winter garb and assuming the more brilliant hues of summer, so the birds under my observation also moulted into the colors appropriate to the season. The old scarlet and black feathers fell from the tanagers and were replaced by others of the same color; from buff, cream and black, the bobolinks moulted into buff, cream and black! There was no exception; the moult was from nuptial to nuptial; not from nuptial to winter plumage. The dull colors of the winter season had been skipped.

I think we thus have proof that the sequence of plumage in these birds is not in any way predestined through inheritance bringing about an unchangeable suc-

cession, in the case of the tanager, of scarlet—green, scarlet—green, year after year, but that it may be interrupted by certain external factors in the environmental complex.

The further significance of these results I leave to others, or until I have more complete data, checked by results derived from control of the other factors of the environment. It would be worse than useless to formulate any theories at the present incomplete stage of the experiments.

The scarlet tanager is of especial interest, as I have said, on account of the absence of such an annual change of color in its near relative, the summer tanager, and experiments with the latter species may shed some light on the subject. Other experiments concerning half and even quarter moults are yielding interesting results and will soon be reported upon.

There is a great satisfaction in thus making even the merest beginning at threshing out these problems, which in their general evolutionary aspect are of far wider application than in the Class Aves alone. And work along these lines is all the more enjoyable because it entails the loss of no life as concerns the birds themselves.

NOTES ON THE BREEDING HABITS OF THE SWAMP CRICKET FROG, CHOROPHILUS TRISERIATUS Wied.

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ABOUT nineteen years ago, Professor O. F. Hay[1] while searching the ponds about Irvington, Indiana, for Ambystomas and their eggs discovered the eggs of *Chorophilus triseriatus*. The eggs were well advanced in development and his observations on the succeeding stages constitute most of what we know of the life-history of the swamp cricket frog.

While on a similar search for *Ambystoma jeffersonianum* in the suburbs of Buffalo one of us found several males and females of Chorophilus and, subsequently, some anuran eggs which for a time remained unidentified. Inasmuch as the identification of these eggs furnished data upon the mating, egg-laying process and fresh eggs of *Chorophilus triseriatus*—the period preceding that of which Professor Hay's observations treat—it seems advisable to present this material.

During the last weeks of March Chorophilus appears in considerable numbers about the outskirts of Buffalo. The male chorus which is easily distinguished from that of *Hyla pickeringii* rises from most of the swamps and temporary ponds, even within the city. The singers themselves, however, are not easily seen, for, upon approach, they become silent and further disturbance causes them to disappear into the vegetation at the bottom of the pond where they remain until some time after the disturbance has ceased. Then, from the most remote corner the chorus is gradually taken up until the whole pond resounds with the ringing notes. In taking up the

[1] Hay, O. P. Notes on the Life History of *Chorophilus triseriatus*. AM. NAT., 23 September, 1899, No. 273, p. 770.

chorus, the assurance evidenced by the single voice is extremely contagious. This fact makes it possible to overcome some of the difficulties which ordinarily present themselves in collecting this species. One has but to place the first captures in a bag or other close receptacle and carry it on one's person. The prisoners chirp up and sing as boldly as though undisturbed in their natural haunt. Their voices elicit an almost immediate response from those in the pond. Indeed, at such a time, with a little practise one can wade about, while they sing on all sides and dip up as many as one desires.

In this way after spending several hours in capturing the first two, 30 specimens, 25 males and 5 females, were taken in less than an hour. These were isolated for the purpose of studying the egg-laying process. On the way from Buffalo to Ithaca (April 1, 1907), they were kept in the same box, but the sexes in separate compartments. During the transit, the males chirped considerably and the females deposited 200 or 300 eggs without attendant males.

The Embrace.—The usual Hyla type of embrace obtains, the forearms of the male being pressed into the axillæ of the female. The males at the height of the breeding period evince an ardor almost as eager as that of the common toad. Sometimes, they embrace each other and as many as 4 or 5 males have been found in one bunch.

A peculiar embrace recorded June 16, 1907, may serve to illustrate how long this nuptial impulse may remain with the male. April 1, 1907, about 30 *Hyla pickeringii*, 1 female, 29 males, and 5 male *Chorophilus triseriatus* were placed in one jar. Between April 1 and June 16, these swamp cricket frogs ate nothing, yet, after $2\frac{1}{2}$ months, and, evidently long past the breeding time, an emaciated male *Chorophilus triseriatus* mated with the single female *Hyla pickeringii*. The embrace was axillary, but sometimes, possibly due to weakened condition, the male partially lost his hold. Then, his arms slipped along on the sides of the body of the female until he came to the lumbar embrace, the arms touching each other on the ventral side. The male disliking this embrace sought

to move along the body of the female to the customary amplexation of his species. A similar weakened condition may explain the occasional records of lumbar embraces with other captive anurans which normally adhere to the axillary type.

At the height of the breeding season the male Chorophilus, like other Anura, often grasp moving objects or animals which are in the same aquarium with them.

The Egg-laying.—On the morning of April 2, 1907, the 25 male *Chorophilus triseriatus* were placed with the five females. At 9:50 A. M., the first mated pair was recorded and, within 20 minutes the female began laying. With one exception, she chose a different perch for each egg-laying period, thus giving a bunch to each period of sexual activity. In one instance she sought the same perch 3 successive times. She ordinarily grasped the branch with her forelimbs. When about to deposit she brought one heel up to the stem and near the vent. Farther back the other foot held the stem with the toes. Each time, just before the voidance of eggs the female raised her anus and the male stretched to bring his vent near that of the female.

This pair consumed 2½ hours in laying a complement of 500 or 600 eggs. The process required about 90 fertilizations and emissions. The intervals between a simultaneous fertilization and emission and a similar succeeding period ranged from 16–35 seconds, the common range 17–30 seconds, the modal time, 20 seconds, the average, 21 seconds. Each time, from 2–10 eggs were voided, being emitted in small strings, a condition which could be most readily seen when occasionally the eggs were unattached to the stem and hung down from the vent of the female. In such cases the strings broke after 10–12 eggs were voided. There were 16 periods of egg-laying, 20–70 eggs being usually laid at a period and each period consumed from 2–7 minutes, 3 minutes being the modal time. Always after a period of laying the pair arose to the surface of the water. These 15 periods of rest varied

from 2–17 minutes, the mode being 4 minutes. All the eggs were laid in water 66° F.

An account of the first pair follows in tabular form:

Number of Sexual Periods.	Length of Sexual Activity.	Intervals Between Periods of Sexual Activity.	Number of Eggs.	Fertilizations and Emissions.	Intervals between Each Emission.
1	3 min	17 min.		8	
2	7 "	4½ "		7	
3	3½ "	5 "	2–7	8	
4	3 "	11 "		9	20, 25, 20, 17, 22, 17, 20, 21 secs.
5	5 "	2 "		14	20, 18, 17, 20, 22, 20, 20, 20 "
6	2 "	2 "		4	18, 20, 18 "
7	3 "	4 "		7	35, 17, 20, 25, 23, 18 "
8	3 "	3 "		6	22, 23, 25, 20, 18 "
9	2 "	16 "		7	20, 20, 22, 17, 17, 17 "
10	4 "	3 "		9	28, 27, 27, 22, 22, 20, 23, 17 "
11	4 "	4 "	2, 2, 3, 3, 7, 4	6	
12	2½ "	10 "		7	
13		6 "	3	1	
14		5 "	2	1	
15		15 "	2	1	
16	1½ "		2, 8, 4	3	

The Eggs.—The second pair were in the embrace at noon. At 1:30 P. M. they began laying and by 4:30 P. M. their complement numbering 600 eggs was laid. The complements of females of *Chorophilus triseriatus* vary from 500–800 eggs. The mature eggs of one ripe female, 3.2 cm. long, numbered 418 for the right ovary, 354 for the left, or a total of 772.

The eggs are laid in bunches and are attached to twigs, branches, fine roots or grass stems. Each bunch contains from 30–100 eggs. An actual count of 5 bunches gave 50, 80, 70, 68, 70, respectively.

The measurements of eggs gave the following results: the average vitellus diameter of 38 eggs was 1.1 mm., the mode, 1.2 mm., the range, .9–1.2 mm.; the average envelop diameter was 5.8 mm., the mode, 5.6 mm., the range usually 5.0–7.8 mm., though sometimes as low as 3.0 mm.

The vegetative pole is white; the animal, brown or black. The envelop about each individual egg makes up the larger portion of the jelly mass of a bunch, yet, there is in addition, some connecting jelly. This has a loose gelatinous consistency and does not envelop the whole mass as in Ambystoma.

MODERN METHODS OF EXCAVATING, PREPARING AND MOUNTING FOSSIL SKELETONS

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The work of collecting and preparing fossil bones is so well known in the museums of America that it is not my intention to explain in detail how to take up bones in the field and to prepare them in the laboratory. Some of the most modern methods adopted in the American Museum of Natural History may, however, be of interest.

FIELD WORK

Too much emphasis can hardly be laid upon the proper treatment of bones in the field, because very crumbly but precious specimens may be saved by proper treatment, while, on the other hand, good specimens may be ruined by wrong treatment.

Up to recent years collectors in the field have used almost exclusively gum arabic for saturating soft bones in order to harden them, and while practical for very porous bones it does not penetrate sufficiently into less porous ones, so that they become hardened on the outside only, remaining crumbly inside. Another disadvantage is that gum will absorb moisture and loses its binding properties in damp weather. Shellac will penetrate the bones much more thoroughly than gum, and when sufficiently dry will leave them much harder and absolutely waterproof. For the last three or four seasons our collectors have used a solution of shellac in place of gum arabic with very good results; and this can be recommended for any field work wherever the fossils are porous and badly preserved. Brown shellac is better as it dissolves more easily and it is stronger, and should be used

wherever practicable, but for light-colored bones white shellac is preferable, as it will not discolor the bones.

PREPARING BONES IN THE LABORATORY

Bones treated in the field with a solution of shellac usually arrive in the laboratory in better preservation than those treated with gum or glue-water, and much less care is necessary to prevent wetting in freeing them from the matrix or burlap cover. Numerous methods are employed to remove the matrix from the bones, according to the condition of the specimens. While a good-sized chisel is practical on a large and well-preserved specimen, small and delicate bones may be freed more securely with so-called harness awls of different sizes, bent and hardened to suit as a gouge and as a scratcher for softer matrix. Wherever the system of pneumatic chisels can be introduced it may be of great importance, especially for lighter chiseling of not too hard rock; it works very rapidly and with less injury to the specimens, as I had opportunity to observe in the Field Museum of Natural History at Chicago.

I have found in my experience that a moderately strong solution of gum arabic used with alabaster plaster is a good and very practicable cement with which to fasten pieces together and is the best cement for all ordinary bones. When used in the right proportions it holds very well, at least as well as the expensive cements, so much advertised. I find that the best and most substantial plaster for restoration work is made by mixing the plaster in a solution of yellow dextrine which can be easily dissolved in boiling water. The dextrine solution should not be too strong; the right strength is indicated when the solution is of a light coffee color. Too much dextrine causes the plaster to crack when dry.

So-called plasterine or modelling clay furnishes a very good material for moulds for rough casting. In this work the bones are slightly coated with glycerine and pressed in both halves of the clay mould in such a way that they

can be lifted out without changing the shape of the mould. The two halves are then placed together properly and filled with plaster, which makes a fairly accurate cast. In many cases I have made the casts larger than the objects by moving the specimen to and fro in the mould to enlarge the cavity. When modelling missing bones much time is saved by casting a bone in this manner and then modifying the form to suit, with knife and awl, instead of modelling the missing bones in clay.

Mounting of Skeletons

The mounting of fossil skeletons is a problem which can not be explained in a general way. Every skeleton has to be treated according to its size, shape, and condition. Skeletons from the size of a cat up to that of a large dog, to be mounted free, can be supported with light soft steel, so that the mounting shows very little. In case the vertebræ are not to be made detachable for study purposes, a flat rod may be run through the neural canal, which makes the neatest mount.

Limbs and ribs supported with flat soft steel, fitted close to the bones, look very well and the mounting is very inconspicuous. All soft bones may be bored and fastened to the supports by screws or pins; harder bones by means of very small flat bands, fitted around the bones and fastened on the main supports with pins or screws.

I may mention another method which I have introduced in the American Museum that may prove to be valuable for other museums. Skeletons which are soft enough, so that the bones can be bored, can be mounted so that every bone is easily detached in the following manner: The back-bone may be supported by a soft steel rod (flat or half round) running under the vertebral column. Fittings to slide over the rod can be cast in bronze without great expense. Each fitting has a pin fastened to it which runs into the centrum of the vertebra, holding it firmly. Pins made stationary by being fastened in the supporting rod do not answer as in many cases it is impossible to get

the individual vertebræ in or out of the column without moving the adjacent vertebræ and pins. After the limbs have been temporarily set up and the flat or half round steel fitted flush to the bones, holes may be bored in the supports and in the bones at the proper places and brass tubes inserted and fastened in the bones with a mixture of shellac and whitening, which holds them very firm. Before the tubes are inserted a thread should be cut inside the tube to which the supports can be screwed very securely. This makes the bones easily detachable. This method is desirable for all skeletons with soft bones, small or large, and especially large skeletons, such as the Mammoth or Mastodon, can be mounted with comparatively few rods or uprights. I can not recommend any style of iron or steel for all purposes as that largely is a matter of individual taste. I myself prefer half round, soft iron for all large skeletons to be fitted along the bones. For very small skeletons, small flat steel is preferable. The so-called channel iron makes good rib supports for all larger skeletons, as there is in the channel a suitable place for the nuts of the screws.

A very practical tool to use in mounting skeletons, especially larger ones, is the "electric drill." It can be attached to any electric light block, and is a great labor-saving tool, which I can recommend very highly. We have one in use in our laboratory which weighs eight pounds; it cuts a ¼-inch hole, can be handled very easily, and can be used to drill holes in any bone or iron without taking them out of place.

Another new feature of importance is the over-head rail or trolley system. As installed in our laboratory, a comparatively heavy rail is fastened to the ceiling, on which trolleys with hoisting blocks attached can be rolled very freely to and fro. Skeletons suspended by these blocks can easily be raised or lowered, or moved from one end of the room to the other. This system is of great importance for economy in mounting very large skeletons. To suspend small skeletons while in operation we use

steel rods screwed to tripods of different sizes for uprights with a horizontal bar fastened by means of clamps, which allow it to be moved up and down. This is a simple apparatus and is very useful for suspending skeletons of not too large dimensions.

To dispense with most of the plumbers' fittings in mounting skeletons we have introduced during the past few years a mode of splitting steel at the end, to act as braces and in other ways, opened and flattened and screwed to the uprights and other supports. This perhaps takes a little more time than to use so-called plumbers' fittings, but it appears as an entirely different style of mounting.

Wherever electric power is available labor-saving machines can be installed, such as drilling machines for heavy work, rotary saws for splitting and cutting steel and brass, small turning lathe attachment for corborundum wheels, and rotary diamond saws for large section cutting. All these appliances just mentioned we have attached to one large lathe run by a one-horse power motor, although a little stronger motor may be recommended. A small gas-blast furnace with a one third or one half horse power motor for the blower makes a sufficiently strong forge to heat a two-inch steel bar and we find this in our laboratory indispensable.

During later years we have introduced numerous other convenient tools, but it would take too long to mention them all here.

ISOLATION AND SELECTION IN THE EVOLUTION OF SPECIES. THE NEED OF CLEAR DEFINITIONS

JOHN T. GULICK

THE discussion concerning the factors in organic evolution has been obscured by the diversity of meanings given to the same terms by different writers, and sometimes by the same writer. What do we mean by isolation, by selection, by environment, by evolution?

DIFFERENT MEANINGS GIVEN TO ISOLATION

I think that in Darwin's books isolation is always used to designate the prevention of free-crossing between different groups by means of factors lying outside of the groups, such as geographical barriers, but it has since been extended to mean the prevention of free-crossing by any means. Professor Kofoid, in his article in *Science* for March 29, 1907, gives the word this broader meaning in one place; but he must use it in a more limited way, when in the last sentence of his article, speaking of what DeVries finds in the elementary species "coincidently appearing" in the evening primrose, he says: "Isolation plays no part in their origin or continuance." I have not found any statement by DeVries maintaining that elementary species remain distinct forms from the original stock, when free-crossing with the original stock continues. In my volume on "Evolution, Racial and Habitudinal," pp. 5, 69–70, 155–156, I call attention to a mutation arising in certain species of snails, and probably producing complete isolation between the new form and the old, though both are occupying the same tree. The hermaphrodite snail is so constructed that it seems impossible for one of sinistral form to cross with one coiled in the opposite way; but in the Hawaiian Islands there are

a number of species presenting both forms. If direct crossing is impossible, it follows that the only chance for continued connection between the two forms is through the subsequent mutation of one or both of the forms; and we know that in some species this occurs in a small percentage of the offspring of each generation.

That isolation is not a necessary condition for the production of this mutation is shown by the fact that it rises suddenly in the midst of an intergenerating group; but the fact that it remains a distinct form, returning to the original form in only a small percentage of the offspring, seems to be due to the fact that by its structure it is prevented from crossing with the original stock. In other words, structural isolation, which is one form of autonomic isolation, produces racial demarcation and initial segregation, opening the way for intensive segregation, through the introduction of divergent forms of selection.

That natural selection is not the cause producing this mutation is shown by the fact that the old form and the new form are equally adapted to the same environment. I, however, maintain that the structural isolation produced by the mutation prepares the way for the introduction of permanently divergent forms of selection.

Different Forms of Selection

In the case of selection as in that of isolation, we find autonomic as well as heteronomic forms. Artificial selection as applied by man to the propagation of domestic plants and animals is a heteronomic factor; and in order to obtain permanently divergent races from the same stock, certain divergent variations or mutations are subjected to divergent forms of selection, while at the same time the different types are artificially isolated, unless there are autonomic factors holding the types apart. Such factors are preferential mating due to sexual and social instincts, or some degree of segregate fecundity; and in plants prepotence of pollen on the stigma of the same type, or flowering at different seasons. Natural selection is a form of heteronomic selection; for, as de-

scribed by Darwin, it is subject to change, only as the group is exposed to changed external conditions resulting in the survival and propagation of an average type differing more or less from the average birth type. Darwin also carefully described one form of autonomic selection, which he called sexual selection. In my volume on "Evolution, Racial and Habitudinal," I have called attention to social and filioparental selection, and several forms of impregnational selection, besides endonomic selection, in which the different methods of using the same environment, adopted by isolated branches of the same species, lead to the survival of different types of variation. These and other forms of autonomic selection must be considered in any complete analysis of the factors producing two or more divergent species from one original species.

VARIATION AND HEREDITY AND THEIR CONTROL

If my analysis of the factors producing divergence is correct, the active cause is found in the powers of variation and heredity possessed by the intergenerating group, while the conditions controlling, shaping and molding the variation and heredity are those that are designated by the terms isolation and selection. Isolation produces demarcational segregation; and divergent forms of selection in the isolated groups will produce intensive segregation, if isolation at the same time continues to hold the groups apart.

Romanes describes selection as a form of isolation, because its influence in controlling variation and heredity is due to its preventing those that survive from crossing with those that perish before propagating. That the influence of both isolation and selection is due to the prevention of free-crossing is certainly true, and, as I have further pointed out, both classes of factors cooperate in producing segregation. It think, however, that it is in better accord with the meaning that writers on natural history have usually given to the two terms to define isolation as the prevention of free-crossing between groups of

organisms *existing at the same time.* In certain cases the isolative process may be selective at the same time; and so demarcational and intensive segregation progress together; as is seen when the strong and courageous migrate together, leaving the weak and timid in the old habitat.

Diversity in the Use of a Complex Environment

An illustration of the wide divergence that may take place in a single family distributed over a small area is found in the Achatinellidæ, a family of snails found only on the Hawaiian Islands. Some genera of this family are found only on the ground, others chiefly on the trunks and branches of the trees, others on the leaves of the trees and shrubs. Ages of divergent evolution have made the individuals of each genus entirely incapable of crossing with those of other genera; but in the case of closely related varieties and species occupying different species of trees in the same valley the conditions are very different. These are cases in which the continued isolation can not be attributed either to external barriers or to physiological incompatibilities. The different methods of using the environment, whether due to habits or to inherited characters, is the real cause of the isolation. Again, of the ten genera of this family some are confined to one or two islands, though the vegetation and other conditions surrounding the family are much the same on the seven islands of the group. The condition explaining the small area occupied by any one of the five hundred species of this family is the limited power and opportunity for migration or transportation; and the great variety of types presented is undoubtedly due, first, to the power of variation possessed by isolated branches of the same species while using like environments in the same way; and second, to the variation in isolated groups introducing divergent methods of using the same complex environment and so subjecting themselves to divergent forms of selection, even when no external barriers hold them apart.

In *Science* for March 30, 1906, Dr. Ortmann refers to species of crawfish subjecting themselves to diverse con-

ditions, in isolated positions, by diversity in their "ecological habits." He describes them as "cases of ecological (or binomic) isolation, where no 'barriers' in the ordinary sense are present." In the relations of Hawaiian snails such cases are not infrequent. Even when the conditions in the environment with which the organism deals are extremely simple, the divergent groups of the original stock may adopt several different methods of dealing with these conditions, and with marked success in the use of each method. A fine illustration of this fact is found in the different species of Triposolenia, a genus of pelagic protozoa described by Professor C. A. Kofoid, in the University of California Publications, Zoology, Vol. 3, Nos. 6, 7 and 8, December 11, 1906. After considering the nature of the several different types found coexisting in the same region, "in the surface waters of the sea," he concludes that, "The utility of each of the complexes of characters is sufficient for their preservation without the necessity of calling in *natural selection* to account for their differentiation and continuance." (See pp. 121, 123.)

CAUSES OF THE EARLIER FORMS OF DIVERGENCE

In the discussion that has appeared in *Science* during the past two years, the chief interest has centered around the question of the causes of the earliest forms of divergence. One method of inquiry has been to observe whether in a given family of organisms the most nearly allied species and races are found in the same or in separate districts. If with great uniformity the nearest allies are found in separate districts, there is good reason to believe that initial demarcation has been due to geographical barriers, or at least to local isolation. If the analysis already given is correct, the first step in divergence must be sought either in some process of migration, or transportation producing local isolation; or in some variation in form, or habits of feeding, or instincts for mating, or time of flowering, or in prepotence of pollen, or in some other quality producing incompatibilities, and so producing

autonomic isolation. In such creatures as snails, it would seem that the different forms of impregnational isolation do not often arise before a considerable degree of divergence has been reached; for usually the most nearly related races, or varieties of Achatinella are found on separate groves of the same species of trees, in different parts of the same valley; while the most closely related groups of varieties, that are classed as separate species, are usually found in separate valleys; though sometimes in the same valley, but living on different species of trees.

In the case of plants, I have seen closely related species growing beside each other, and in some such cases they are found to flower at different months of the year, and in other cases it would probably be found that they are held apart by the prepotence of pollen of a given species on stigmas of the same species. In some of these cases where the present form of isolation is undoubtedly autonomic, it may be impossible to say whether the new type was not first developed in a few individuals, that for a generation or two were partially isolated geographically or locally in some sheltered nook.

Do New Types Continue in Spite of Free-Crossing?

As we have already shown in certain species of Hawaiian snails, a sudden mutation may arise, which by its very constitution is prevented from crossing with the parent stock; and in such cases it is evident that a permanent type may begin with the mutation. But is there any proof that a mutation that freely crosses with the original stock will remain unchanged, each type thriving and remaining unblended with the other? If the mutation is the dominant form, it may be granted that it will in time overwhelm the original form; but can two closely related races or species freely cross with each other, for many generations, without either type being affected by the process? For an answer to this question I would refer the reader to an article by Robert Greenleaf Leavitt in The American Naturalist for April, 1907. On pp. 214–217 he gives quotations from Professors Davenport,

Castle and Forbes, showing that "Everywhere unit characters are changed by hybridizing." This testimony is chiefly from those who have experimented with the crossing of animal forms, but even in the case of plants, there is reason to believe that when free-crossing continues divergence is checked. There is reason to believe that even with plants the controlling factor in each case of continuously divergent evolution is either some form of heteronomic isolation or some form of variation introducing autonomic isolation.

MORITZ WAGNER'S THEORY AND MY THEORY WERE ISOLATED AND DIVERGENT FROM THE BEGINNING

Moritz Wagner, in his "Law of the Migration of Organisms," was the first to insist on the importance of geographical isolation as a factor in evolution, but when he asserted that without geographical isolation natural selection could have no effect in producing new species he went beyond what could be sustained by facts. My own theory, though it did not take form till four years later, was reached without any knowledge of his, and therefore in complete isolation from his; and when they came together for comparison they were found to be quite divergent.

In March, 1868, Moritz Wagner read a paper before the Royal Academy of Sciences at Munich on "The Law of the Migration of Organisms," and in 1873 an English translation of a fuller paper by him entitled "The Darwinian Theory and the Law of the Migration of Organisms" was published by Edward Stanford, of London. It was through this pamphlet that I became acquainted with his theory concerning the impossibility of the production of new species except when and where migration establishes a colony geographically isolated from the original stock. In this paper we read: "The constant tendency of individuals to wander from the station of their species is absolutely necessary for the formation of races and species" (p. 4). "Where there is no migration, that is, where no isolated colony is founded, natural

selection can not take place" (p. 59). These and many other passages of similar import indicate how fully he recognized the importance of isolation, and how at the same time his theory was a denial of some of the facts in the origin of species. The following are some of the facts with which his general theory as well as his special statements were in conflict:

1. That, through change of climate and of other conditions due to geological changes, the whole fauna and flora of an island like Iceland might be subjected to new forms of selection producing a complete change of many species into new species, without any chance for migration. After the publication of my article in *Nature,* July 18, 1872, in which I emphasized the importance of isolation, I met Darwin at his home, and he called my attention to Wagner's theory, and suggested that it did not correspond with the facts of nature, especially on this point.

2. That the influence of geographical isolation in producing divergence, and in opening the way for selection to cooperate in producing divergence, is wholly due to its prevention of free-crossing, and that the same result may, in various ways, be brought about by divergent habits or instincts, or other incompatibilities, while the isolated groups remain in the original habitat of the species.

3. That divergence does not necessarily require the influence of different forms of selection.

4. And that different forms of selection do not necessarily depend on exposure to unlike environments; for diversity in the forms of selection may be due to diversity in the methods of using the same environment adopted by isolated branches of the same species.

In August, 1872, I read before the British Association for the Advancement of Science a paper on "Diversity of Evolution under One Set of External Conditions,"[1] in which the conditions just mentioned were briefly stated. In two subsequent papers entitled "Divergent Evolution through Cumulative Segregation," and "Intensive Seg-

[1] This paper was soon after published in the Linnean Society's *Journal,* Zoology, vol. XI, pp. 496–505.

regation," read before the Linnean Society in 1887 and 1889, and published in their *Journal,* the subject was more fully discussed, and since then in my volume on "Evolution, Racial and Habitudinal," published by the Carnegie Institution, my view of the factors of organic evolution has been presented, with special relation to their interaction on each other, and the close correlation between the evolution of habits and the evolution of racial characters. It is to this last-mentioned phase of the subject that I have hoped that I might call special attention. I regard this influence of acquired habits in the control of the forms of selection as of great importance, especially in the evolution of the higher classes of animals, and in the races of mankind.

MEANING OF THE TERM ENVIRONMENT

In all my discussions, I have been careful to give a uniform meaning to the term environment. When treating the evolution of species, or of smaller groups of intergenerating organisms, the environment is, in my language, always the set of influences lying outside of the group under discussion, and is never used to designate the influence of one part of the group upon another part, as, for example, the influence of parents upon offspring, of males upon females, of the strong upon the weak. In the generalizations made by some writers, it is impossible to decide whether the environments referred to are intended to include these reflexive influences or not. But even with the broadest interpretation of the term environment, I can not accept the statement often made that there is no divergence in branches of the same species unless they are exposed to different environments.

Such a conclusion seems to be based on the assumption that all transformation in organisms is due to adaptations giving more or less advantage to the forms that survive, and ignores the fact that in many species there are countless variations of a non-utilitarian character. It also fails to recognize the fact that isolated groups of individuals of the same variety, exposed to the same external

environment, and also to the same internal influences producing selection, may still, before many generations have passed, adopt different methods of dealing with the external environment, or introduce divergent forms of sexual or social selection, or of some other form of reflexive selection. The divergence, in such cases, is explained by the power of the species to vary, and by the probability that the variation will introduce new methods of meeting surrounding conditions. F. W. Headley, in his volume on "Problems of Evolution" (on pp. 146–149), gives illustrations of how branches of the same species may adopt *"alternative methods of adjustment to the same environment,"* and yet in the same book (on p. 103) we read: "If the environment remains unchanged, evolution ceases," and on p. 153—"Nothing but change of environment can lead to further evolution." His mind seems to cling to the old statements of general laws, though he has come to recognize a class of facts that are quite at variance with these old statements.

It therefore appears that we need not only a clear and consistent use of terms, but a clear and consistent statement of the facts of the organic world, in their bearing upon the changes that take place in organisms. I have carefully studied O. F. Cook's article in *Science* of March 30, 1906, and his previous papers to which he refers in that article. The chief difference in our estimates of the factors of evolution seems to me to result from a difference in the meanings that we give to the word evolution. In my use of the word all changes and divergences in the inherited and acquired characters of organisms are included. The chief factors I find to be variation and heredity in an intergenerating group moulded and controlled by isolation and selection. Fuller statements will be found in my book on "Evolution, Racial and Habitudinal," pp. 60, 79–80, and 138. Of these factors Dr. Cook says that variation and intergeneration relate to evolution, but isolation and selection, though "factors of species-formation, are not at all factors of evolution." It is evident that this difference in our enumeration of the factors of evolution is due to the different meanings that we give to the term evolution.

NOTES AND LITERATURE

EVOLUTION AND HEREDITY

Darwinism To-day.[1]—"Charles Darwin was the foremost scientific man of the entire nineteenth century, and I think he must also be termed the greatest Englishman of his time. Even the very few persons who would assign to the famous naturalist a less solitary preeminence must admit that his ability was of the highest order." Such an estimate of Darwin, recently expressed by Professor Minot, is seldom presented in discussions of *Darwinism*. Those using this term must explain that they do not mean the origin of coral islands through subsidence of the ocean floor, or the overturning of the earth by worms, or the adaptations of plants to cross-fertilization, or even organic evolution, but that they have in mind natural and sexual selection and perhaps also pangenesis. The recent book by Professor Kellogg is a discussion of the various theories of evolution.

The first chapter introduces the reader to the "philosophic turmoil and wordy strife," very little of which is said to have found its way into current American literature. In the second chapter it is stated that the "millions of kinds of animals and plants can have had an origin in some one of but three ways; they have come into existence spontaneously, they have been specially created by some supernatural power, or they have descended one from the other in many-branching series by gradual transformation. There is absolutely no scientific evidence for either of the first two ways; . . . If such a summary disposal of the theories of spontaneous generation and divine creation is too repugnant to my readers, . . . then my book and such readers had better immediately part company; we do not speak the same language."

There is little depth in such a statement. It will be generally conceded that existing animals have descended from the past,

[1] Kellogg, V. L. Darwinism To-day. A discussion of present-day scientific criticism of the Darwinian selection theories, together with a brief account of the principal other proposed auxiliary and alternative theories of species-forming. New York, Henry Holt and Company, 1907. 403 pp. $2.00.

and that at some remote time one or many forms first appeared upon the earth. Some will say that they appeared spontaneously and others that they were a divine creation, just as present occurrences are regarded by some as spontaneous and by others as divinely ordained. However, that the debate should not be checked by philosophy, the author hastens to consider the various attacks on "Darwinism," the defense, and finally other theories which may be substituted. His style is breezy, such as Englishmen describe as American, and New Englanders as Western.

"Sexual selection is one of Darwin's supporting theories which has nearly gone quite by the board." In support of this Mayer's convincing experiments with *Callosamia promethea* are fully described. "If there is any moth species in which the colors and general pattern of the male ought to be readily obvious to the female . . . it is this species." Mayer found that the females did not prefer normal males to those from which the wings had been clipped, or to those on which the red-brown wings of the female had been fastened in place of their own black ones of very different shape. The author believes that a satisfactory explanation of sexual dimorphism is yet to be formulated.

The importance of selection in producing mimicry in color patterns is accepted, though somewhat doubtfully. Professor Kellogg says of Basilarchia—"But thanks to its perfectly mimicking color-pattern, it wings its deceitful way unmolested. There is huge usefulness here, and selection can well be the steadfast maintainer of the viceroy's dissimulation." The marring of the resemblance by the dark streak across the hind wings is noted but not accounted for; the "over-refined" resemblance of Kallima to a leaf is called "absurd." The author leaves his reader to draw his own conclusions in regard to mimicry and many other problems. Thus Bumpus is cited to show that a storm destroys the physically defective sparrows, and Kellogg shows that a drought destroys the fit and the unfit fish. The reader must judge whether it is variation or "hard luck" which usually brings destruction.

Three theories alternative with selection are presented, namely, "Lamarckism," orthogenesis, and heterogenesis (mutation). Darwin is cited in favor of all three. Lamarck's conception of evolution is "a great thought and a clear one," but it lacks

experimental support. Likewise for the theory of heterogenesis as capable of explaining species formation as a whole, the author finds an "extreme meagerness in quantity of the real scientific evidence." He declares that no indubitable cases of species-forming or transforming have been observed.

"The theories of orthogenesis of the general type exemplified by Eimer's are directly in line with the spirit of modern biological methods and investigations. They rest on the assumption that physico-chemical factors produce direct effects on the plastic organism, and that such effects . . . modify or control evolution." Any tendency, such as is shown by Nägeli, to substitute a "mystic vital force" for the "physico-chemical factors" receives the author's severe censure; yet except as one emphasizes the complex and unknown internal factors rather than the simpler conditions of environment, these conceptions are not far apart. "Nägeli believes that animals and plants would have developed about as they have, even had no struggle for existence taken place, and the climatic and geologic conditions been quite different from what they actually have been." Much more could be said in favor of orthogenesis than Professor Kellogg records.

In the concluding chapter it is stated that "Darwinism, then, as the natural selection of the fit, the final arbiter in descent-control, stands unscathed, clear and high above the obscuring cloud of battle. . . . To my mind every theory of heterogenesis, of orthogenesis, or of modification by the transmission of acquired characters confesses itself ultimately subordinate to the natural selection theory." Yet before closing, Professor Kellogg returns to a discussion of orthogenesis as "a determinate though not purposeful change."

After each chapter there is an appendix containing considerable citations from works on evolution. The volume should prove valuable to students; we hope that they will not lay it aside with the author's remark "*Kurz und gut,* we are immensely unsettled."

F. T. L.

The Effect of Environment upon Animals.—It is well known that if the pupæ of certain butterflies, *e. g.*, Vanessa or Pyrameis, be subjected to extreme cold (0° to — 20° C.) many of the adults will be aberrant in color pattern. However, if they be subjected to extreme heat (42° to 46° C.) the same aberrations

will be produced. Less extreme heat (35° to 37° C.) gives aberrations differing from these. Opinions do not agree as to the reason why extreme heat and extreme cold produce the same results. M. von Linden considers it to be a "pathological" phenomenon caused by tissue injury. Narcotizing and whirling on a centrifugal machine cause similar effects. Fischer[1] argues with great force that this is not so. He believes it to be a "normal" arrest of development, such as occurs during hibernation, pointing out, however, the difficulty of drawing a sharp line between normal and pathological physiology. Both Vanessa and Pyrameis are common in America. It would be well worth while to study critically the inheritance of these abnormalities.

Salamandra maculosa is normally either viviparous or oviparous, producing a large number (up to 72), young. These young, when born, are larvæ. They live in water for some time, finally losing their gills and metamorphosing into land salamanders. If, however, the female be deprived of water, she will give birth to a small number (2 to 7) of young which have already lost their gills. Kammerer[2] carried the experiment still farther and found that, even if the abnormally born females be given water, they give birth to young having reduced gills.

Plate[3] has made a detailed study of the genus Cerion (land snails) of the Bahama Islands. Many local races or varieties were found. He believes these to be due to the modifying influence of the environment, but gives no experimental evidence. Snails could easily be transplanted from one island to another in order to test this point. The Bahama Islands are so near to America that this problem should appeal especially to American students of evolution.

FRANK E. LUTZ.

[1] Fischer, E. Zur Physiologie der Aberationen- und Varietaten-Bildung der Schmetterlinge. *Archiv für Rassen- und Gesellschafts-Biologie,* IV, 6, November–December, 1907.

[2] Kammerer, Paul. Die Nachkommen der spätgebornen *Salamandra maculosa* und der frühgebornen *Salamandra atra. Archiv für Entwicklungsmechanik der Organismen,* XXV, 1 and 2, December, 1907.

[3] Plate, C. Die Variabilität und die Artbildung nach dem Prinzip geographischer Formenketten bei den Cerion-Landschnecken der Bahama-Inseln. *Archiv für Rassen- und Gesellschafts-Biologie,* IV, 4 and 5, July–October, 1907.

THE PROTOZOA

Some Recent Protozoa Literature.—Waves of special enthusiasm sweep over the domain of biology as of other sciences; each leaves its mark, passes on and is followed by others. At one time it was the "section cutters" at another the "finger bowl brigade," at present it is genetics. Some investigators are independent enough to swim in quieter waters while some are so bold as to try to make an independent high-water mark long after the wave has passed. To the later group Hartmann and Prowazek must be assigned, for in a recent paper[1] they deal with the homologies of the centrosome, a problem which has never been solved and one that can not be regarded as obsolete, but which is no longer on the wave of biological enthusiasm.

Nor is the point of approach at all novel. They see in the nucleus and centrosome of the higher cell types only the reminiscence of a dual condition in protozoa. To be sure, they bring to bear a great fund of recently published observations, more particularly on protozoan cell structures, and they see in the metazoan nucleus and centrosome the outcome of dimorphic nuclei in these primitive animals. The two nuclei of the hypothetical ancestral form are not of the type suggested by Schaudinn in the early advocacy of this same theory (*Amœba binucleata*), but of the type seen in Trypanosoma, where trophonucleus and kinetonucleus are persistent morphological elements of the cell. They believe that the same dual arrangement is present in other protozoa; in some the kinetonucleus is reduced to a mere granule outside of the normal cell nucleus (as in the Centralkorn of the Heliozoa); in others the two nuclei are united to form an "amphinucleus," the one encased within the other as in the typical centronucleus. Here is the only really novel point in their discussion, and this can not be accepted, for to assign to the division center in a nucleus of the Euglena type the rôle of an independent nucleus is a *reductio ad absurdum*. The authors use a considerable area of printed matter to prove that these kinetoplasmic structures in protozoa are homologous with the centrosomes of higher forms, a point of view generally accepted more than a decade ago; and certainly nothing new is gained

[1] Hartmann and Prowazek. Blepharoplast, Karyosom und Centrosom. *Arch. f. Prot.*, X, 2–3.

by calling these division centers "nuclei." The one feature in support of this view is the presence of chromatoid material about the blepharoplast in Trypanosoma and in Paramœba, but even the truth of this is not generally accepted, Schaudinn's observations not having had sufficient confirmation to warrant universal acceptance. The authors' statement that chromatin material is likewise present in the great sphere of Noctiluca is not true. On the whole this conception of blepharoplast, karyosome and centrosome gives an inadequate summary of the striking recent advances in protozoan morphology and leaves the problem of the origin of the metazoan centrosome very much as it was ten years ago.

The pioneer work of Schaudinn's upon which this conception of Hartmann and Prowazek's is based has not been fully and satisfactorily confirmed, while much of it has been denied. Novy, for example, has continually fought against the double intra- and extra-cellular life of *Trypanosoma noctuæ* and now Moore and Breinl,[2] working with different kinds of *Trypanosoma*, find that the nuclei of *T. gambiense*, *T. brucei* and *T. equinum* all conform to the centronucleus type and that the blepharoplast or kinetonucleus (Woodcock) arises in the latent bodies by halving of the intra-nuclear division center and without any accompanying chromatin such as Schaudinn described in the case of *T. noctuæ*. Passing over the fact that the present authors somewhat stultify themselves on the perfection of their technique and give an ungenerous blanket criticism of all others who have worked upon the morphology of trypanosomes, it must be admitted that their criticism is to a certain extent justified, for the majority of observers have made too free use of the dry smear method. The so-called chromosomes of the trypanosomes, for example (not chromosomes at all in the strict sense), are interpreted by Moore and Breinl as irregular masses of chromatin which may assume any form under the rough processes of the dry method of fixation. This may or may not be true, but at any rate the figures given by the English authors and representing the finer structures of these nuclei do not inspire confidence in the methods which they themselves advocate, although they are, indeed, well tried and recognized methods.

[2] Moore and Breinl. Cytology of the Trypanosomes. *Annals of the Liverpool School of Tropical Medicine*, 1, No. 3.

Apart from this question of technique, upon which the last word is not yet given, Moore and Breinl bring forward evidence which throws a new light on the life history of *T. gambiense,* the cause of sleeping sickness. They find a phase in the life history where the nucleus, surrounded by a small bit of protoplasm, is left over after the bulk of the trypanosome has degenerated. This nucleated bit, which they name the "latent body," is stored up in the spleen and bone marrow of the experimental animal (rat), ultimately reappearing in the circulation where a new, young trypanosome arises from it. They find no evidence of trimorphic differentiation which Schaudinn first described for *T. noctuæ,* but they call attention to the fact that a complete series of sizes of trypanosoma may be selected, and claim that the indifferent, male, and female, forms are only arbitrarily chosen individuals from such a series.

Another interpretation is given to the trypanosomes with long chromatin bars such as Prowazek in the case of *T. lewisi* regarded as male forms. The English observers introduce a new hypothesis to account for this, viz., that it represents a type of autogamous conjugation. The bar is of kinoplasmic material growing out from the blepharoplast to the nucleus, where a portion of its substance, as they believe, unites with the nucleus. The suggestion is ingenious and, in view of the constantly growing evidence in favor of autogamy in other kinds of protozoa (Entamœba, Actinosphærium, *Amœba proteus,* etc.), must be taken into account.

On *a priori* grounds it would certainly seem that if conjugation among trypanosomes is a normal part of the life history, and there is no reason to believe it absent, it would be more frequently observed and there would be no uncertainty about it. Its infrequency and the doubt existing in regard to the observations that have already been made lead us to suspect that conjugation of some obscure type occurs here. In flagellated protozoa where conjugation of the ordinary type is characteristic, the periodicity of conjugation is one of the most noteworthy features. This is well illustrated in a timely article by C. Clifford Dobell on the life history of a simple Peranema-like flagellate which he names *Copromonas subtilis.*[3] The flagellate is a com-

[3] Dobell, C. Clifford. The Structure and Life History of *Copromonas subtilis* nov. gen. et nov. sp., a Contribution to our Knowledge of the Flagellata. *Q. J. M. S.,* No. 205, 1908.

mon parasite of the rectum of frogs and toads and grows readily, the author observes, in rectal contents with normal salt. Conjugation between similar organisms (isogametes) occurs from the seventh to the ninth day of such a culture, the result being either an encysted form (permanent cyst) or a motile form which reproduces by division for several generations and then encysts.

The trypanosomes evidently present no such simple life history as this which Dobell describes and, although accumulating evidence makes it probable that all stages are confined to the single host in the greater number of cases at least, every description of conjugation thus far published is so fantastic as to arouse suspicion. What is true of trypanosomes is even more characteristic of spirochætes, a field of research so difficult that very few have had the hardihood to publish accounts of conjugation, and needless to say none that has been published is acceptable. The latest on Spirochæta is a paper by H. B. Fantham on the relatively large spirochæte of the oyster and clam.[4] This *Spirochæta balbianii*, which was monographed by Perrin a couple of years ago, is interesting in having a central helix of chromatin which is spirally wound, and upon which larger granules of chromatin are suspended at intervals. This represents an intermediate condition, so far as the nucleus is concerned, between the isolated granules of chromatin in bacteria and in certain forms of Spirochæta (*e. g., S. obermeieri*), and the formed nuclei of higher types of protozoa. Reproduction both of this form and of *S. anodontæ* is by longitudinal and occasionally transverse division, both types occurring according to the author. Conjugation in no form was observed. Like the majority of recent writers on the spirochætes, Fantham proposes a new group for them intermediate between the protozoa and the bacteria. He suggests that they be made a new "class" of organisms under the name "Spirochætacea." Such innovations, however, can do no good and it is far better not to further confuse an already mixed up classification. When the full life history of the genus (or genera) of Spirochæta is known it will be time enough to change the classification.

These flagellates are not the only forms of protozoa over

[4] Fantham, H. B. *Spirochæta* (*Trypanosoma*) *balbianii* (Certes) and *Spirochæta anodontæ* (Keysselitz). Their Movements, Structure and Affinities. *Q. J. M. S.*, No. 205, 1908.

which there is much discussion and controversy at the present time. The rhizopods offer quite as extensive a field for divergent opinions and here again it is mainly in connection with the parasitic types. The life histories of the ordinary forms are being slowly established and with this basis the parasitic forms should be comparatively simple to work out. The one remaining important step to be made in working out the life history of the common rhizopod *Arcella vulgaris* has quite recently been taken by W. Elpetiewsky,[5] and it is fitting that it should have been made in Hertwig's laboratory, where the first important steps were taken. The author finds that gametic nuclei are formed from the distributed chromidia in the way described by Schaudinn for Centropyxis, and by Schaudinn and Lister for Polystomella. Macrogametes and microgametes are formed and conjugation of two such anisogamous swarmers was followed step by step. He found furthermore, that Arcella reproduces also by the formation of pseudopodiospores, and that these develop fine heliozoa-like radiating pseudopodia, upon the ends of which they roll about for a period of from two to three hours. This observation is interesting in the light of the possible origin of the lobose rhizopods from the heliozoa.

It is not quite so simple a matter to accept the latest work on the parasitic rhizopods and we entirely disagree with Prowazek[6] in his conception of the so-called group Chlamydozoa. In this proposed new group of protozoa which he would place intermediate between the protozoa and the bacteria, Prowazek places the majority of the recently contested forms of disease-producing organisms. The disputed organisms of variola, vaccinia, scarlet fever, trachoma, rabies, *Molluscum contagiosum*, and some others of less importance are all grouped together here apparently without regard to their morphology or effects upon the host. All of these organisms are regarded as extremely small cell parasites which are made conspicuous by reason of a more or less thick secretion of nuclear material about them, the name of the proposed group being based upon this characteristic (χλαμυς—mantle).

In this supposition the author takes a great deal for granted and begs two very important questions, first, that the inclusions

[5] W. Elpetiewsky. Zur Fortpflanzung von *Arcella vulgaris* Ehr. in *Arch. f. Prot.*, X, No. 2–3, 1907.

[6] S. Prowazek. Chlamydozoa. In *Arch. f. Prot.*, X, No. 2–3, 1907.

are organisms, and second, if organisms, that the bulk of their substance is to be traced to nuclear secretions. The limits of the present reference will not permit an extensive analysis of Prowazek's different assumptions, but one or two matters may be pointed out as showing his method of treatment, and incidentally his ignorance or, possibly, disregard, of careful work of others. The organism of rabies, for example, exists, as do all rhizopod protozoa in many different sizes, and one form of the organism is extremely minute. This small phase is characteristic of the so-called "fixed virus" and has been entirely overlooked by Prowazek despite the accurate and detailed work of Dr. A. W. Williams and others. In another phase the organism is quite large and characteristically amœboid in form. Prowazek finds none of these larger forms in centrifuged virus and concludes that the intra-cellular phase is absent in the virus thus treated, and since he failed to see these forms in the fixed virus he further concludes that the bulk of the Negri body in rabies must be a nuclear secretion and that the organisms are the minute brightly staining points (chromatin) of the larger forms which are actually present in the fixed virus and in centrifuged virus, but invisible. In this conclusion he shows not only a total disregard for what other competent workers have done, but a surprising ignorance of the actual structure of the Negri body.

Apart from special criticisms which might be carried out for each of the diseases mentioned, the general criticism may be made that it is not good zoology to create a group in classification while there is still some doubt as to the organisms being living things; and it is not good cytology to assume an entirely new function (of specific secretions) in various cells in response to such questionable organisms. The present critic believes, indeed, that these questionable structures are organisms, and organisms belonging to the rhizopod group of protozoa, but not to any group with the characteristics of the proposed "Chlamydozoa."

G. N. C.

EXPERIMENTAL ZOOLOGY

The Determination of Sex in Frogs.—Few results in experimental biology have been more puzzling than those involving the question of the determination of the sex of the frog. The earliest

observations—those of Born—seemed to indicate that the food given to the young tadpoles determined the sex of the frog. Yung also obtained about 70 per cent. of females when his tadpoles were well fed. Balbiani and Henneguy have stated that tadpoles fed on egg-yolk produced more females than those fed on a vegetarian diet. On the other hand, Cuénot obtained no such results, and the recent careful and extensive experiments of Miss King have shown clearly for the toad that the nutrition of the tadpole has no influence on the sex of the adult. Despite the fact that these recent results go far towards showing that sex is not determined or even altered by food relations, a curious disproportion of the sexes in frogs has been noted by several observers. The recent valuable experiments of Richard Hertwig do not, in the opinion of the reviewer, bear out the interpretation that Hertwig has placed upon them. Nevertheless, his methods give promise, if further extended, of throwing light on the problem.

In Hertwig's first contribution to the subject published in 1906 he suggested that sex is determined by the condition of *ripeness* of the egg at the moment of fertilization. This view is not new, and Hertwig's attempt to connect his view with the ratio of nucleus to cell-plasm of the egg at different periods of its maturation can hardly be looked upon favorably, since in the frog's egg the nucleus as such has already disappeared when the egg leaves the ovary. The chromosomes are thereafter arranged on the equatorial plate of the first polar spindle. It is, however, during this period that the degree of ripening is supposed to determine the sex of the egg. However unsatisfactory this specific suggestion of Hertwig may now appear, the possibility must still be granted that in some way the degree of maturity of the egg may have an influence on sex-determination. Hertwig interpreted his experiments to mean that at first the egg *tends* to produce males, then during the middle phases of its ripening it tends to produce females, and finally during its later phases again its tendency is towards male production. It is not our purpose to discuss in detail this interpretation, but it may be stated that Hertwig's experiments fell far short of proving his hypothesis.

In Hertwig's second paper,[1] to which we wish more especially

[1] Hertwig, R. Weitere Untersuchungen ueber das Sexualitätsproblem. *Verh. Deutsch. Zool. Gesell.*, 1907.

to call attention, he also brings forward the same hypothesis and attempts to explain certain incongruities of the two series by other suggestions. It will be noticed that while the "older" eggs give an enormously high percentage of males, those first fertilized also give an excess of males or at least equal numbers of the two sexes. There is no middle register in which females are in excess.

Hertwig's principal results are shown in the accompanying table. The eggs of three females, 1, 6, and 10, were fertilized at four different intervals (I, II, III, IV) of several hours apart (6, 18, 30, etc.); the percentages show in each case how many males developed to each 100 females—the actual number of individuals employed standing above the percentages. The striking fact shown by the table is the high percentage of males throughout, but especially towards the end of each series, where in one case there were 129 males to 17 females.

	I	II	III	IV
	— 6 —	— 18 —	— 30 —	
1.	34♀ : 47♂	65♀ : 77♂	156♀ : 194♂	7♀ : 48♂
	141%	119%	124%	685%
	— 36 —	— 18 —		
6.	64♀ : 61♂	101♀ : 139♂	115♀ : 169♂	
	95%	137%	147%	
	— 18 —	— 24 —	— 22 —	
10.	55♀ : 52♂	148♀ : 87♂	71♀ : 70♂	17♀ : 129♂
	100%	59%	100%	759%

The results leave little doubt that there is something in this series that stands for maleness. A number of possibilities besides the one adopted by Hertwig will suggest themselves. There is, moreover, one vital weakness in the experiment as carried out, for which, unfortunately, there is no control—different males were used, apparently, at least for the last fertilization, and the percentage of male-producing sperm present in these males was not determined. Without this control the experiment is seriously defective. Hertwig himself has realized this deficiency and has carried out one successful experiment in which the eggs of one female—separated into lots—were fertilized by different males. The results are not convincing, as the following statement shows.

The eggs of a female from a locality (Lochausen, indicated by L in the table), where the season was nearly at its end, were separated into six lots. Three of these were fertilized by sperm

from three males of the same locality (indicated by l^1, l^2, l^3, in the table), and the other three were fertilized by sperm of three males from another locality (Schleissheim, = S in diagram). The converse experiment was also carried out. The results are given in the next table, in which the double sign ♀♂ indicates that the sexual organs were in an indifferent condition. It will be observed that a very large number of individuals are referred to this category. Hertwig states that in those cultures that developed best there was a decided excess of males—more than of indifferent forms. On the other hand, the poor cultures contained females almost exclusively, fewer indifferent forms and no males.

	l'	s'	l^2
L.	2♀♂ : 31♀	9♀♂ : 53♀	80♂ : 77♀♂
S.	9♀♂ : 65♀	†	77♂ : 73♀♂

	s^2	l^3
L.	176♂ : 156♀♂	
S.	10♂ : 75♀♂	9♂, 59♂♀ : 65♀♂, 11♀

Hertwig thinks that the results show that the sperm has a distinct influence on sex-determination. He suggests that in the present case the eggs were nearly in a condition of equilibrium so that a *slight* influence on the part of the male sufficed to turn the scales. He adds that it is thinkable that as a rule the eggs at the time of normal fertilization have their sex so positively determined that the relatively small influence of the male has no influence. It will be noted, however, that in Hertwig's own experiment the condition of the two females selected was very different, yet there is a surprising similarity in the results produced when the males that fertilized the eggs are considered.

The experimental results are not sufficient to give any positive light on the question, but the method that Hertwig has employed in the last experiment is one that promises to give an answer to the question whether the egg or the sperm determines the sex in the frog.

If one may hazard a guess, the results of Hertwig's experiments seem to show that the male is responsible for sex-determination. Since normally all the eggs are fertilized it can not be assumed that, if they are of two sexes, those of one sex are preponderatingly injured or killed by the cold of winter. In regard to the sperm, however, it is possible that more of one kind,

if two kinds exist, are injured or that internal processes may lead to the production of more functional sperm of one sex. These factors may differ in different individuals or be characteristic of different races or regions. The importance of settling this question and the ease with which the experiment can be carried out with the simplest possible apparatus ought to lead many naturalists to repeat the experiment in different localities and with different species. The only difficulty arises from the mortality of the tadpoles; for they must be kept until the time of metamorphosis (which, however, for the wood frog, the toad and for some of the tree frogs takes place as early as June of the same year). By keeping the tadpoles in running water, or by changing the water in the dishes every day, success is assured.

M.

ANATOMY

Wiedersheim's Comparative Anatomy.[1] The various forms and editions of this work have been for two decades, we believe, the most used and useful text-books upon the comparative anatomy of vertebrates. In the ten years since the publication of the second English edition, three progressively larger German editions have appeared, and the book became so large that Wiedersheim published a résumé entitled "An Introduction to Comparative Anatomy." The third English edition is, in both size and substance, a compromise between the second English and the large German editions. The text proper occupies one hundred and ten pages more than in the second edition. This is due partly to the addition of new matter and partly to the use of uniform type in the text, instead of printing in smaller type the matter assumed to be less worthy of the student's attention. This change has improved the appearance of the book and the increase in size has been partly counterbalanced by printing more compactly and in smaller type the much extended and useful bibliography.

New facts have been incorporated, usually and unfortunately without recasting, but the sections upon the skin, skull, brain-

[1] Comparative Anatomy of Vertebrates. Adapted from the German of Dr. R. Wiedersheim, by W. N. Parker. Third edition, founded on the sixth German edition. 576 pp., 372 figures. The Macmillan Company, 1907.

membranes and "adrenals" have been essentially rewritten. As a result, the book is improved by many small increments as well as by the new treatment of a few subjects.

Among these is the interesting physiological difference between the lungs of birds and of mammals, now properly noted for the first time. In mammals during inspiration the lung expands and draws into its blind terminal respiratory chambers a mixture of fresh and residual air. The residual air greatly dilutes the oxygen which comes in contact with the absorbing blood vessels, and also prevents the carbon dioxide from being expired directly. In birds the lung is a network of anastomosing tubes which are not expansile. Fresh air is drawn through these tubes by the expansion of the air sacs, which are non-respiratory terminal prolongations of the lung. The lung of the bird may, in a sense, be compared with the respiratory bronchioles of mammals, the mammalian alveoli corresponding with the avian air sacs. Thus the lung of birds is peculiarly adapted for the rapid oxidation correlated with the requirements of flight and with a high body temperature. Other additions of this sort contribute to the value of this edition.

L. W. WILLIAMS.

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